An Integrated Approach to Delimit Species in the Puzzling *Atractus emmeli* Complex (Serpentes: Dipsadidae)

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ABSTRACT: We evaluated the taxonomic status of snakes from the *Atractus emmeli* species complex (composed by *A. boettgeri, A. emmeli, A. paravertebralis,* and *A. taeniatus*) on the basis of concordance between quantitative (meristics and morphometrics) and qualitative (pholidosis, color pattern, and hemipenis) analyses of morphological characters, in combination with ecological niche modeling and niche overlapping. We synonymize *A. boettgeri*, *A. paravertebralis*, and *A. taeniatus* with *A. emmeli* based on the congruent analytical results. We also describe a new species to accommodate the Brazilian populations from the state of Mato Grosso mainly based upon some unique states of morphological characters, including hemipenial morphology, color pattern, and meristics. We found that the new species has a distinct ecological niche compared with *A. emmeli* and some level of niche overlapping with *A. albuquerquei*. We found great differences in ecological niches of species occurring in the Cerrado versus those occurring in the Western Amazon–Andean foothills, suggesting a putative niche evolution in this group.

Key words: *Atractus boettgeri*; *Atractus paravertebralis*; *Atractus taeniatus*; Ecological niche modeling; Hemipenial morphology; Linear morphometry; Parecis Plateau; Population character frequency

Accurate species delimitation is one of the most challenging tasks in Systematic Biology because cladogenesis results in lineages comprising a series of unconcluded phenomena, such as reciprocal monophyly, gene coalescence, reproductive isolation, ecological divergence, and/or morphological distinctiveness (Mayr 1942; de Queiroz 1998; Sites and Marshal 2004; Knowles and Carstens 2007). For that reason, any arbitrary criterion alone or a preconceived set of rules defining species (e.g., phenotypic or genotypic distances) could fail to satisfy scrutiny of the hypothesis testing depending on the properties of the organism involved (de Queiroz 1998, 1999; Camargo and Sites 2013; Teske et al. 2018) or even geographic representativeness of samples and population structure (Sukumaran and Knowles 2017). On the other hand, poorly defined species ultimately increase the burden of the taxonomic inflation (see Meire and Mace 2007), which has negative impact on the fields of macroecology and macroevolution, as well as strongly influencing the conservation agenda (Isaac et al. 2004; Mace 2004). Besides, in organisms displaying cryptic morphology, fine-scaled endemism, incomplete sampling, and/or absence of obvious reproductive barriers, it is particularly difficult to accurately establish species boundaries using only one line of evidence (Padial et al. 2010; Rivera et al. 2011).

The cryptozoic snakes of the genus *Atractus* Wagler 1828 are distributed widely in the Neotropics, occurring from Panama to Argentina (Giraudo and Scrocchi 2000; Myers 2003). *Atractus* is the richest genus among extant snakes and currently comprises 140 recognized species (Passos et al. 2018a,b). In the past 10 yr, the taxonomy of the genus has undergone an unprecedented flux of changes based on a series of reviews and species descriptions (see Passos et al. 2018c and references therein). As an expected result, old and poorly characterized taxa have been resurrected (Passos et al. 2010a) or rediscovered (Passos and Arredondo 2009). These discoveries were based on reidentification of misidentified samples in collections (Passos and Lynch 2011; Passos et al. 2018c) and through new collections made after original descriptions (Passos et al. 2010b, 2016a; Vanegas-Guerrero et al. 2014), or a combination of both (Passos et al. 2007a; 2009a; 2010a; 2012; 2013a,b; 2016b; de Fraga et al. 2017). In contrast, the evaluation of many recently hypothesized species has revealed an astonishing number of junior synonymies (Kok et al. 2007; Passos et al. 2009d, 2010c, 2012, 2013b, 2018c; Passos and Prudente 2012), complicating the already challenging task of assessing diversity and phylogenetic relationships of *Atractus* (Passos et al. 2017).

In this paper, we use qualitative (color pattern and hemipenes) and quantitative (meristics and morphometrics) analyses of putatively independent phenotypic character systems, coupled with ecological niche modeling to infer species boundaries and evaluate the taxonomic status of old names available to *Atractus emmeli* species complex.

HISTORICAL RÉSUMÉ

Boettger (1888) described *Atractus emmeli* on the basis of two specimens from "Mapiri" (= Mapiri River, tributary of Beni River, ca. 15°18′S, 68°12′W, 630 m, Department of La Paz, Bolivia; datum = WGS84 in all cases), distinguishing it from *A. occipitoalbus* (Jan 1862) by having, among other features, seven supralabials and two postoculars (vs. eight supralabials and single postocular in *A. occipitoalbus*). Boulenger (1896) reported new specimens of *A. emmeli* from the localities of "Para" (supposedly from the state of Pará, Brazil; the collector, Emilio Goeldi, a traveling collector from the Museu Nacional lived in Belém, Pará), Charobamba (ca. 14°37′S, 68°43′W, 733 m, Department of Cochabamba) and "Campolican" (= Rurrenabaque, 14°26′S, 67°32′W, 212 m, Department of Beni), both in Bolivia. Boulenger (1896) reported on new specimens of *A.*

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maculatus (Günther 1858) from localities of Charobamba (see above), "Aschiquiri" (= Achiquiri, ca. 15°10′S, 68°14′W, 700 m, Department of La Paz) and "Yungas" (ca. 16°20′S, 45°13′W, 300–1500 m, between Department of La Paz and Cochabamba; see Paynter 1992), all in Bolivia. Boulenger (1896) described *A. boettgeri* based on a specimen from Yungas, apparently considering that the three species *A. boettgeri, A. emmeli,* and *A. maculatus* occurred sympatrically in the region of Yungas and Charobamba (see above) in Bolivia. Boulenger (1898) described *A. balzani* based on a single specimen collected by L. Balzan in "Missiones Mosetenes" (= Covendo Mission range, 15°47′S, 66°58′W, 517 m), Bolivia.

Griffin (1916) named *Atractus taeniatus* based on an individual from Santa Cruz de La Sierra (17°49′S, 63°09′W, ca. 420 m, Department of Santa Cruz, Bolivia), comparing it in detail with *A. roulei* Despax 1910 (a species restricted to Pacific foothills of the Ecuadorian Andes; see Passos et al. 2013c). Schmidt and Walker (1943) recorded *A. emmeli* in Peru based on a female specimen with 188 ventrals and 22 subcaudals (specimen location not traced), but lacking specific provenance data. Peters and Orejas-Miranda (1970) listed *A. emmeli* as having 15 or 17 dorsal scale rows in their matrix of characteristics from members of the genus *Atractus*. McCoy (1971), based on additional samples of *A. boettgeri* from Santa Cruz de La Sierra and *A. taeniatus* from Buenavista (17°27′S, 63°39′W, ca. 394 m, Department of Santa Cruz, Bolivia), proposed the synonymy of both, highlighting that they only differed slightly in meristic and color pattern features for which considerable ontogenetic and sexual variation are reported for other congeners. Furthermore, McCoy (1971) pointed out that the name *A. boettgeri* should be used, at least provisionally, for the specimens from Department of Santa Cruz, because a third species from Department of Beni (*A. emmeli*) may be also related to this complex and has precedence in terms of priority over all these other names. Apparently, McCoy considered that all these species might represent a single evolutionary unit.

Henle and Ehrl (1991) described *Atractus paravertebralis* on the basis of a specimen from "Baja(o) Tambopata" (authors employed both spellings; lower Tambopata River, SW from Puerto Maldonado, 12°36′S, 69°14′W, 200 m, Department of Madre de Dios) in Peruvian Amazonia, comparing it with *A. ventrimaculatus* Boulenger 1905 (a species endemic from Mérida mountain range in Venezuela) and *A. vertebralis* Boulenger 1904 (a species with 17 dorsal scale rows from Peruvian Andes highlands). Henle and Ehrl (1991) distinguished *A. paravertebralis* from other congeners in Peru (among them *A. emmeli*) by 'a distinct general color pattern' and 15 dorsal scale rows. Williams and Gudynas (1991) resurrected *A. taeniatus* based on 6 individuals with 15 dorsal scale rows from Entre Rios and Misiones Provinces of Argentina. Williams and Gudynas (1991) pointed out that Argentinian samples conform well to characters found in *A. taeniatus* and that McCoy's arguments to previous synonymy were unjustified.

Silva (1993) reported on two specimens from Candeias do Jamari (08°48′S, 63°41′W, 90 m, state of Rondônia, Brazil) as *Atractus* cf. *taeniatus*. Fernandes (1995) reviewed the *A. reticulatus* Boulenger 1885 complex and considered *A. paraguayensis* Werner 1924 a valid species, but did not

include the Argentinean specimens (previously revalidated as *A. taeniatus*) in his study. Vanzolini (2000) proposed the synonymy of *A. paraguayensis* with *A. reticulatus*, although with no justification. Giraudo and Scrocchi (2000) reported on new specimens of *A. paraguayensis* from southeastern Paraguay and northeastern Argentina, but they identified specimens from northwest Argentina as *A. taeniatus*, according to Williams and Gudynas (1991).

Passos et al. (2010c) established that populations associated with semideciduous forests along the Paraná River basin, previously identified as *Atractus taeniatus* in Brazil and Argentina, correspond to *A. paraguayensis*. Salazar-Bravo et al. (2010) reported a new record of *A. boettgeri* from a locality 1.4 km N of San Pablo (15°14′S, 63°52′W, 195 m, Department of Beni, Bolivia) and briefly commented on the taxonomy of Bolivian forms of *Atractus* related to *A. emmeli* (*A. boettgeri, A. emmeli,* and *A. taeniatus*). These authors recognized all three Bolivian species previously mentioned in literature: *A. boettgeri, A. emmeli,* and *A. taeniatus*. Quinteros-Muñoz (2013) reported a new record of *A. occipitoalbus* from Valle de Sacta (17°06′48.6″S, 64°45′52.0″W, 223 m, Department of Cochabamba, Bolivia), as a second record of *A. occipitoalbus* in Bolivia (previously included by Fugler 1983, 1984 [in Fugler and Cabot 1995] in the Bolivian fauna but without mention of voucher specimens). Quinteros-Muñoz mentioned that *A. occipitoalbus* is distributed from Colombia to Peru and Bolivia. However, Passos et al. (2010a), in the revision of the *A. occipitoalbus* species complex, established that the range of *A. occipitoalbus* includes only Colombia and Ecuador, highlighting that specimens previously reported as *A. occipitoalbus* from Peru belong to a different taxon (see *A. emmeli* remarks). Finally, Passos et al. (2018a) proposed the synonymy of *A. balzani* with *A. emmeli* on the basis of overlapping of phenotypic characters previously used by Boulenger (1898) for diagnosis of *A. balzani*.

Materials and Methods
Material Examined

Institutional abbreviations are those of Sabaj (2016). Data from additional specimens of *Atractus* examined in previous published studies by the first author can be found in Passos et al. (2005a; 2007a,b; 2009a–e; 2010a–c; 2012; 2013a–d; 2016a,b; 2017; 2018a–c), Passos and Fernandes (2008), Prudente and Passos (2008, 2010), Passos and Arredondo (2009), Passos and Lynch (2011), Passos and Prudente (2012), Schargel et al. (2013), Almeida et al. (2014), Salazar-Valenzuela et al. (2014), and de Fraga et al. (2017). We prepared fully everted and almost maximally expanded hemipenes from four specimens and examined in situ partially or fully everted (but not maximally expanded) organs from four additional specimens (Appendix). We provide the authorship and date only in the first mention of each name.

Geographical Data

Coordinates of localities were acquired by consulting original data in museum catalogues, digital databases or geographical gazetteers (Stephens and Traylor 1983; Paynter and Traylor 1991; Paynter 1992; IBGE 2011). We refined, when possible, the provenance of records obtained from the

literature or in museum databases without specific field coordinates using the software Google Earth Pro v7.1.2 (https://www.google.com/earth/versions/).

Techniques for Phenotypic Characters

Terminology for cephalic shields follows Savage (1960) as augmented by Peters (1964), whereas ventral and subcaudal counts follow Dowling (1951). Condition of the loreal scale follows Passos et al. (2007b). Measurements were taken with a dial caliper (Mitutoyo) to the nearest 0.1 mm, except for snout–vent length (SVL), caudal length (CL), and total length (TL), measured with a ruler to the nearest 1 mm. Measurements and descriptions of paired cephalic scales are based on the right side of the head. Sex was determined by subcaudal incision. We examined maxilla in situ under a Stemi 2000C (Zeiss) stereoscope, through a narrow latero-medial incision between the supralabials and the maxillary arch. After removing tissues covering the maxillary bone, we counted teeth and empty sockets. Method for preparation of preserved hemipenes was modified from Pesantes (1994) in replacing potassium hydroxide solution with distilled water (see Passos et al. 2016a). Prior to the inflation with petroleum jelly, the organs remained 15 min in an alcohol solution of Alizarin red to stain the ornamented calcareous structures according to an adaptation from original procedure used by Uzzell (1973) and modified by Harvey and Embert (2009). Terminology for hemipenial descriptions follows Dowling and Savage (1960) and Zaher (1999), with few minor adaptations (sensu Passos et al. 2013d). We follow Passos et al. (2009e) and Passos et al. (2010c) with respect to conditions of the morphological characters used in diagnosis and descriptions.

Species Concept and Diagnosis Criteria

In this study, we followed the general lineage species concept of de Queiroz (1998, 1999). We consider presence of one or more exclusive apparently fixed diagnostic characters (either morphological or ecological), which distinguishes a given taxon from the others in the *Atractus emmeli* complex, as species delimitation criteria. Nonetheless, the sample sizes assessed here were too small for statistical tests of qualitative characters (sensu Wiens and Servedio 2000); therefore, we looked for concordance between the discrete and continuous characters, as well as corroboration with niche modeling. Some of these features are likely uncorrelated (but see Results and Discussion), so the correspondence between these kinds of data might represent independent evidence for species delimitation. However, in the cases of putatively diagnostic discrete characters, we explicitly searched for congruence with another line of evidence to increase the confidence in each taxonomic decision (see Passos and Fernandes 2009; Passos et al. 2010a).

Operational Analytical Units

We considered putative natural barriers (e.g., rivers) and geographic proximity of the available samples to evaluate levels of distinction among populations. We used the major tributaries from the Amazonas River and Paraná River basins as natural barriers to dispersion among populations. Group 1 included specimens from east of the Beni River, considered as *Atractus taeniatus*. Group 2 included specimens from Bolivia and Brazil along tributaries of the Madeira River to the right bank of the Beni River, formally *A. emmeli* and *A. boettgeri*. Group 3 comprised populations of the Amazon Basin of Peru from Madre de Díos River to Amazonas River, here attributed to *A. paravertebralis*. We grouped *A. emmeli* and *A. boettgeri* in a single operational group because there is no clear morphological difference (see McCoy 1971) and no obvious geographical disjunction between these species. However, the population from Parecis Plateau, Mato Grosso, Brazil, was considered a unique group because these displayed some apparent morphological differences (see Results).

Quantitative Analyses

We evaluated the assumptions of univariate normality by inspection of normality plots and homocedasticity through a Levene test (Zar 1999). In cases where characters showed insufficient variation to justify these assumptions, we performed nonparametric tests or excluded such variables from the analyses (Zar 1999). We performed a Principal Component Analysis (PCA; see Manly 2000), an exploratory procedure to evaluate the quantitative discrimination between currently recognized species that were hypothesized mainly on the basis of discrete differences (e.g., general color pattern according to Henle and Ehrl 1991). We projected the first two components onto orthogonal axes and computed 95% confidence regions from the simulation of 1000 pseudoreplicate data matrices obtained by parametric bootstrap (Efron 1979; Manly 2000). All principal components loadings were portrayed as vector correlations (directional cosines), which were estimated for each variable by correlations with projection scores across individuals (Wright 1954). This procedure reveals the original variable closely correlated with main axes of variation (Strauss 1985). We estimated missing values through the estgroup function in MATLAB software, which estimates the missing data based on variance–covariance matrix for each group defined on the basis of geographical proximity. Individuals or variables with missing data above a cutoff of 20% were not considered in the statistical analyses. We used the following variables for statistical analyses: number of ventral scales, number of subcaudal scales, number of dorsal scales at the level of second subcaudal, number of supralabials, number of infralabials, number of gular scales, number of preventrals, number of maxillary teeth, and SVL/CL ratio. We performed all analyses using the software MATLAB v4.2c1 (MathWorks 1994).

Qualitative Analyses

We plotted the distribution of qualitative characters (pholidosis, color pattern, and hemipenial morphology) based on population frequency from each character state along the distribution of the *Atractus emmeli* complex. On the basis of the distribution of apparently independent discrete characters, we investigated whether trends to fixation or loss of a given attribute exist in each population, according to ideas of Brownian motion applied to Biology (see Felsenstein 1985). We also searched for congruence between these groups and current taxonomy (including *A. boettgeri, A. taeniatus,* and *A. paravertebralis*). The discrete characters (or discretized variables due to the small sample size) evaluated were number of postocular, supralabial, and

infralabial scales; number of maxillary teeth; head coloration in dorsal, lateral, and ventral views; body coloration in dorsal and ventral views; coloration of ventral surface of tail; length of hemipenial lobes (discretized variables); level of hemipenial capitulation (discretized variables); height of bifurcation of the sulcus spermaticus (discretized variables); sulcus spermaticus orientation; level of thickness of the sulcus spermaticus and development of the sulcus spermaticus edges; concentration of lateral spines on the hemipenial body and at the intrasulcar region (both discretized variables); and level of development of vertical walls of distal calyces.

Niche Modeling

We obtained most distribution data of the *Atractus emmeli* complex from collection data associated with voucher specimens housed in the scientific collections. We included literature records only when literature data allowed identification of the specimens with a reasonable level of precision through mention of unique combination of morphological features (McCoy 1971; Quintero-Muñoz 2013). The resulting database includes 62 locations with confirmed presence of individuals of the *A. emmeli* complex. In this study, we attempted to minimize the spatial autocorrelation of data by using nonadjacent presence records (see below). We also included a data set of putative closely related species (*A. albuquerquei;* see Passos et al. 2010c), which displays a parapatric distribution along the Brazilian Shield, in order to better understand the effective niche parameters of the *A. emmeli* complex.

To predict the ecological niche of both *Atractus albuquerquei* (a putative closely related species; see Passos et al. 2010c) and *A. emmeli,* we imposed a minimal distance of 50 km among presence records to reduce possible issues related to the spatial auto-correlation and sampling biases, using the Program R package spThin (Aiello-Lammens et al. 2015). This procedure resulted in 25 unique records for *A. emmeli* and 30 unique records for *A. albuquerquei.* We then restricted the background for niche modeling to an area extending up to 10° around the distribution points of the clade *A. emmeli + A. albuquerquei,* which also more or less includes the distribution of the remaining species in this species group (i.e., *A. reticulatus* and *A. caete;* Passos et al. 2010c). We randomly produced pseudoabsences within the background areas (10 times the number of presences of each species).

We downloaded 19 bioclimatic layers (10 arc-minute resolution) from chelsa-climate.org. This data set is based on current climatological models of atmospheric circulation, complemented by interpolated data, an important methodological improvement for predicting climate conditions in regions with few meteorological stations such as the Amazon forest and western Brazil (Karger et al. 2017). We also downloaded layers of soil variables from soilgrids.org (Hengl et al. 2014), for a total of 21 environmental predictors. Layers of soil variables (the first 15 cm of the soil surface) were aggregated by average to 10 arc-minute resolution and included (1) percentage of clay, and (2) percentage of sand. We tested for multicollinearity among all predictors using Variance Inflation Factor (VIF) with the R package usdm (Naimi et al. 2014), excluding all predictors with VIF-values >10. From this selection, two soil predictors plus eight climatic predictors remained. To keep the balance of at least five presence records per predictor and avoiding over-parameterization of the models (Agresti 2007), we restricted the number of predictors to five, because *Atractus emmeli* presented 25 unique point-localities. We then selected the two soil predictors related to the fractions of sand and clay, plus three climatic predictors with low VIF values that we have considered as presenting more potential to influence the geographic distribution of those species: Bio16 = Precipitation of Wettest Quarter, Bio17 = Precipitation of Driest Quarter, and Bio3 = Isothermality. We downloaded the same set of WorldClim climatic predictors for the Last Glacial Maximum (about 22,000 years ago; Community Climate System Model 4; Braconnot et al. 2007).

To predict the ecological niches of the selected species, we used three different modeling algorithms: Generalized Additive Models, Generalized Linear Model, and Random Forest (Elith et al. 2006; Elith and Graham 2009; Heikkinen et al. 2012). We generated 20 replications for each technique using cross-validation and bootstrapping to validate the models. From the resulting models, we produced an ensemble forecasting weighted by the Area Under Curve statistics (Araújo and New 2007), and we calculated the predictive performance of the models using the True Skill Statistics (Allouche et al. 2006). We then visually checked whether there was any geographical overlap between the model predictions of the selected species and the occurrence records of the Mato Grosso population.

To test the niche overlap in the environmental space, we performed niche overlap analyses among *Atractus albuquerquei, A. emmeli,* and the Mato Grosso population using the PCA-env approach (see Broennimann et al. 2012). This method uses a PCA to transform correlated variables into a reduced linear representation of all variables. Therefore, we included all 21 climate and soil variables described above. In this analysis, a density distribution is estimated from the presence records with a kernel density function. The Mato Grosso population is represented by only four localities, so we added a buffer of 50 km around the records to estimate its environmental space. Niche overlap was measured using Schoener's D metric (Schoener 1970), which ranges between 0 (no niche overlap) and 1 (complete niche overlap). The significance in niche overlap (D metric) was accessed using randomization tests referred to as niche equivalency and niche similarity (Warren et al. 2008; Broennimann et al. 2012). We obtained niche equivalence by shuffling the occurrence records of both species in 100 iterations and calculating D metric for each replication. Niche similarity is measured by randomly moving the whole density of occurrence records of one of the species each time within the available climatic space 100 times, calculating the D metric for iteration. We performed all tests in R using the scripts provided by Broennimann et al. (2012).

Results

Quantitative Analyses

The *Atractus emmeli* complex shows significant sexual dimorphism in the number of ventral scales ($F_{1,56} = 37.5$; $P < 0.001$), subcaudal scales ($F_{1,57} = 38.8$; $P < 0.001$; $n = 60$) and SVL/CL ratio ($F_{1,57} = 88.3$; $P < 0.001$), and therefore these characters must be treated separately for each sex in all
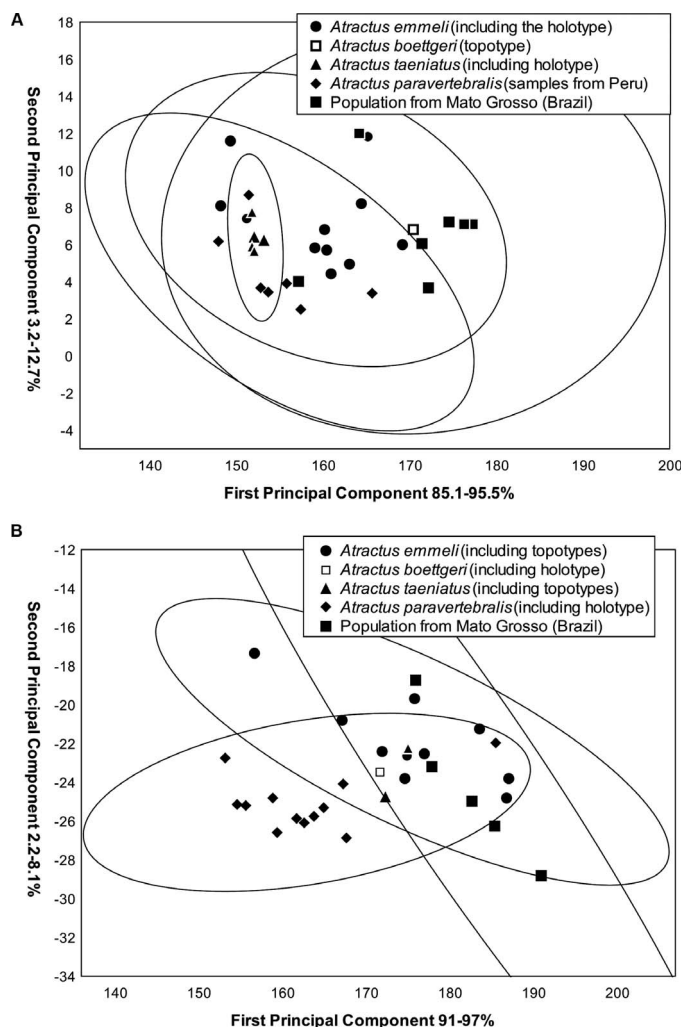
FIG. 1.—Bivariate plot with 95% confidence regions and 1000 bootstrap pseudoreplicates for the first two axes derived from scores of Principal Component Analysis for males (A) and females (B), with directional cosines. Percentages accompanying title for each axis represent the amount of variance from the data set explained by each principal component. The original variables are as follows: numbers of ventral scales, subcaudal scales, and maxillary teeth; and caudal length/snout–vent length ratio. The first principal component axis was strongly correlated with the number of ventrals, and the second axis with the number of subcaudals and snout–vent length/caudal length ratio both in males and females.

subsequent analyses. Nonetheless, these three variables, despite approaching a normal distribution, were heteroscedastic, probably because of differences in the sample size for each group. Our samples from some populations also contained different numbers of males and females. The assumptions of normality and/or homoscedasticity were violated, so we refrained from performing nonparametric analyses of variance and preferred to carry out a PCA on a strictly exploratory basis (Manly 2000). The projections of the bivariate plots based on scores of PCA for males and females (Fig. 1) were unable to discriminate the two groups established a posteriori. The slight discrimination occurred mainly in the first principal component axis, which was strongly correlated with the number of ventrals and SVL/CL ratio both in males and females (see Fig. S1 in the Supplemental Materials available online).

Qualitative Analyses

The diagnoses of *Atractus emmeli, A. boettgeri, A. taeniatus,* and *A. paravertebralis* were based exclusively on external morphological traits (i.e., meristic data from scale counts and color pattern). All these features fall entirely within the variability observed in the populations attributable to *A. emmeli.* Moreover, other characters previously employed for distinction of the above taxa in literature (pholidosis characters mentioned in Salazar-Bravo et al. 2010), displayed some variance in some populations but were not fixed in any population sampled or showed large overlap among the currently recognized species (Fig. 1), as follows:

Meristic characters.—Although the number of maxillary teeth and supralabial scales has been employed to distinguish between taxa in the *Atractus emmeli* species complex (Griffin 1916; McCoy 1971; Salazar-Bravo et al. 2010), the first two features are currently polymorphic at the population level. Despite a tendency of a higher incidence of six supralabials in Bolivian samples (Table 1), the frequency of seven supralabials was greater in all populations sampled in our study. Furthermore, the putative occurrence of larger number of maxillary teeth in *A. taeniatus* has no geographical basis because all topotypes examined have six or seven teeth and the single specimen with eight teeth on one side of the maxilla comes from a Peruvian specimen (MUSM 11144; Table 1).

Color pattern.—We found that some characters show distinct population frequencies (i.e., condition of the pale parietal band and ventral coloration), but they are far from being fixed at a population level (Figs. 2–10). Furthermore, other coloration features examined in the types and/or topotypes of *Atractus boettgeri, A. paravertebralis,* and *A. taeniatus* entirely overlap the pattern of populations here attributable to *A. emmeli* (Figs. 2–10). Although *A. paravertebralis* displays a spotted pattern not observed in the types and in the entire Peruvian sample (Fig. 2C vs. Fig. 4), such a pattern is also widespread within Bolivian populations, revealing a local gradient of dorsal dimming (Fig. 9E–F). Besides obvious difficulties with darkened specimens in collections (because methods of fixation and time and mode of preservation may affect the general coloration especially with respect to carotenoid pigments), within available samples this color pattern is not unique and does not display any apparent geographical structure.

Hemipenial morphology.—The analysis of hemipenis variation revealed some apparently exclusive and geographically fixed characteristics between Mato Grosso and other populations of the *Atractus emmeli* complex. Some characters of shape and ornamentation, such as level of bilobation and orientation of the lobes, calyces concentration, development of capitation groove, and thickness of the sulcus spermaticus, were distinct within a single population (Fig. 11). We believe that none of the differences observed on the ornamentation were caused by preparation artifacts affecting general hemipenial shape (see Passos et al. 2016a for additional discussion). Although we examined a limited sample of each population, we prepared organs under distinct conditions (retracted, partially or fully everted in the field or laboratory) in each population and the observed differences were congruent (Fig. 11). Additionally, the general hemipenial morphology of the Mato Grosso

TABLE 1.—Variation in selected meristic and morphometric characters for populations of the *Atractus emmeli* complex. The range of variation of each continuous variable is from our own sample plus Quintero-Muñoz (2013) and Salazar-Bravo et al. (2010). In parentheses, mean ± 1 standard deviation follows ranges. For variables lacking secondary dimorphism we placed both sexes together. SVL = snout–vent length; CL = caudal length.

Variable	Group 1		Group 2		Group 3		Mato Grosso population	
Sex	Males (n = 7)	Females (n = 3)	Males (n = 11)	Females (n = 12)	Males (n = 7)	Females (n = 11)	Males (n = 5)	Females (n = 5)
Ventrals	151–169 (155 ± 7.3)	173–183 (177 ± 5.3)	148–168 (158 ± 8.9)	156–187 (175 ± 5.3)	147–157 (154 ± 5.8)	154–185 (164 ± 2.9)	170–176 (173 ± 2.5)	175–192 (182 ± 6.8)
Subcaudals	22–31 (25 ± 3.1)	19–22 (21 ± 1.6)	23–31 (25 ± 2.3)	20–25 (22 ± 1.7)	20–26 (22 ± 1.7)	14–25 (16 ± 2.9)	26–28 (27 ± 1.0)	20–26 (22 ± 1.9)
CL/SVL ratio	10.0–14.7 (11.4 ± 1.6)	7.8–8.5 (8.1 ± 0.4)	10.2–14.2 (11.6 ± 1.2)	7.6–9.6 (8.3 ± 0.7)	9.2–11.9 (10.4 ± 1.0)	5.7–7.4 (6.8 ± 0.9)	8.1–10.4 (9.5 ± 1.2)	7.4–9.7 (8.6 ± 1.0)
Supralabials	6 (32.2%), 7 (67.8%)		6 (53.3%), 7 (46.7%)		6 (2.8%), 7 (94%), 8 (2.8%)		7	
Infralabials	7		7 (97.8%), 8 (2.2%)		7		7	
Maxillary teeth	6 (7.8%), 7 (92.8%)		7		6 (25.7%), 7 (74.3%)		7	
Postoculars	1 (11%), 2 (89%)		2		2		2	

TABLE 2.—Summary of values obtained for all niche models performed. ROC = receiver operating characteristic.

Species	Method	Area under the ROC curve	True skill statistics
A. albuquerquei	Generalized Additive Models	0.81	0.62
A. albuquerquei	Generalized Linear Models	0.84	0.67
A. albuquerquei	Random Forest	0.87	0.72
A. emmeli	Generalized Additive Models	0.77	0.58
A. emmeli	Generalized Linear Models	0.79	0.55
A. emmeli	Random Forest	0.84	0.64

population is more similar to that of *A. albuquerquei* than those from any other population of *A. emmeli* (see comparisons).

Niche Modeling

All models for *Atractus albuquerquei* and *A. emmeli* presented Area Under Curve values ranging from 0.77 to 0.87 (Table 2), indicating a reasonable performance of the models. The True Skill Statistics results for the models of both species were also satisfactory, always >0.55 (in a scale from −1 to +1), indicating low rates of commission and omission errors (Table 2). The prediction of suitable areas for *A. emmeli* indicates a predominantly western Amazonian and Beni savannas distribution, without geographical overlap with the records of the Mato Grosso population (Fig. 12A). The projection of the models of *A. emmeli* to the Last Glacial Maximum indicates that areas with higher suitability were more widespread in the Amazon Basin in the past, but only low suitability values were predicted within the area currently occupied by the Mato Grosso population (Fig. 12B). The predicted niche for *A. albuquerquei* shows a more coincident distribution with most of the Cerrado savannas, geographically overlapping with the Mato Grosso population (Fig. 12C), with few changes in such pattern since the Last Glacial Maximum (Fig. 12D).

The niche overlap analyses using PCA-env approach indicated that there is no significant overlap between the environmental niches of *Atractus emmeli* and the Mato Grosso population (D metric = 0.021; niche equivalence $P = 1$; niche similarity randomization $P = 0.33$; Fig. S2 A–B in the Supplemental Materials available online). For *A. albuquerquei* and the Mato Grosso population there is a significant but relatively low overlap in their environmental niches (D = 0.25; niche equivalence $P = 1$; niche similarity $P = 0.04$; Figs. S2 C–D in the Supplemental Materials available online). This indicates that the environmental niche occupied by the ranges of these species is more similar to each other than expected by chance, which would be anticipated because of the geographical overlap in their distributions. There is no significant overlap in the niches of *A. albuquerquei* and *A. emmeli* (D = 0.318; niche equivalence $P = 0.82$; niche similarity $P = 0.10$; Fig. S2 E–F in the Supplemental Materials available online).

Taxonomic Decisions

Exploratory morphometric analyses corroborate that all groups defined a posteriori cannot be segregated by the principal axes of the PCA, which were most correlated with size (SVL/CL ratio and number of subcaudal scales) and form (number of ventral scales; Fig. 1). Although qualitative analyses
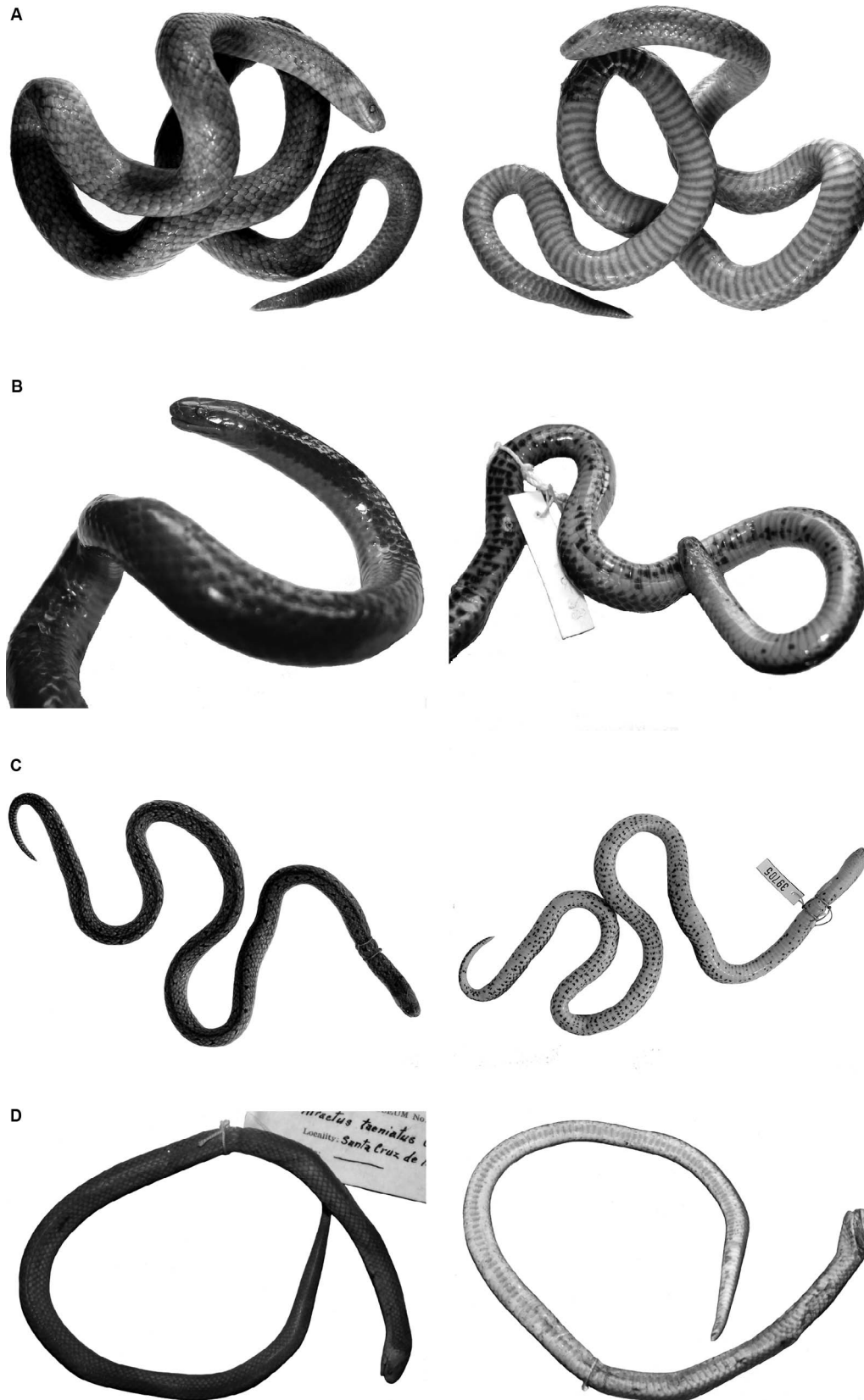
F<small>IG</small>. 2.—Color pattern on dorsal and ventral views of body of *Atractus emmeli* (A; SMF 19364, lectotype, juvenile male, 290 mm snout–vent length [SVL], 35 mm caudal length [CL]) from Mapiri River, Department of Beni, Bolivia; *A. boettgeri* (B; BMNH 1946.I.6.29, holotype, adult female, 325 mm SVL, 26 mm CL) from Yunga, La Paz–Cochabamba Department boundaries, Bolivia; *A. paravertebralis* (C; ZFMK 39705, holotype, adult female, 450 mm SVL, 40 mm CL) from "Baja Tambopata" (= lower Tambopata River), Department of Madre de Dios, Peru; and *A. taeniatus* (D; CM 117, holotype, adult male, 218 mm SVL, 22 mm CL) Santa Cruz de la Sierra, Department of Santa Cruz, Bolivia.
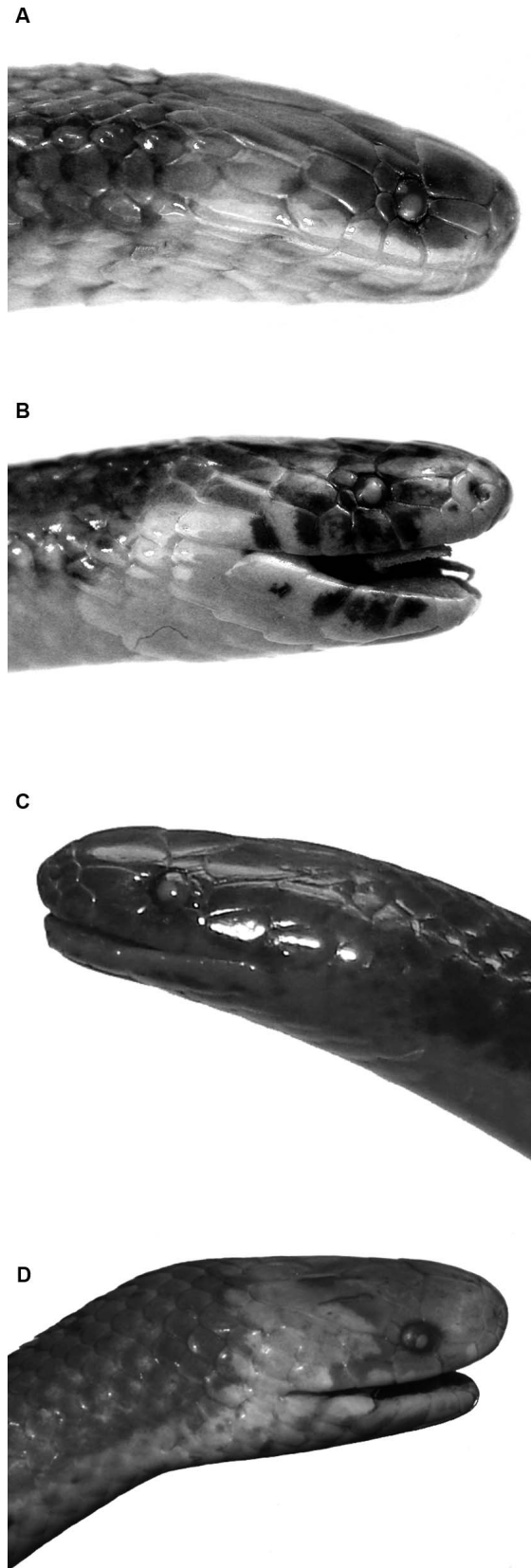
FIG. 3.—Color pattern of lateral views of head of *Atractus emmeli* (A; SMF 19364, lectotype, juvenile male, head length 11 mm) from Mapiri River, Department of Beni, Bolivia; *A. paravertebralis* (B; ZFMK 39705, holotype, adult female, head length 14 mm) from "Baja Tambopata" (= lower Tambopata River), Department of Madre de Dios, Peru; *A. boettgeri* (C; BMNH 1946.I.6.29, holotype, adult female, head length 10.4 mm) from
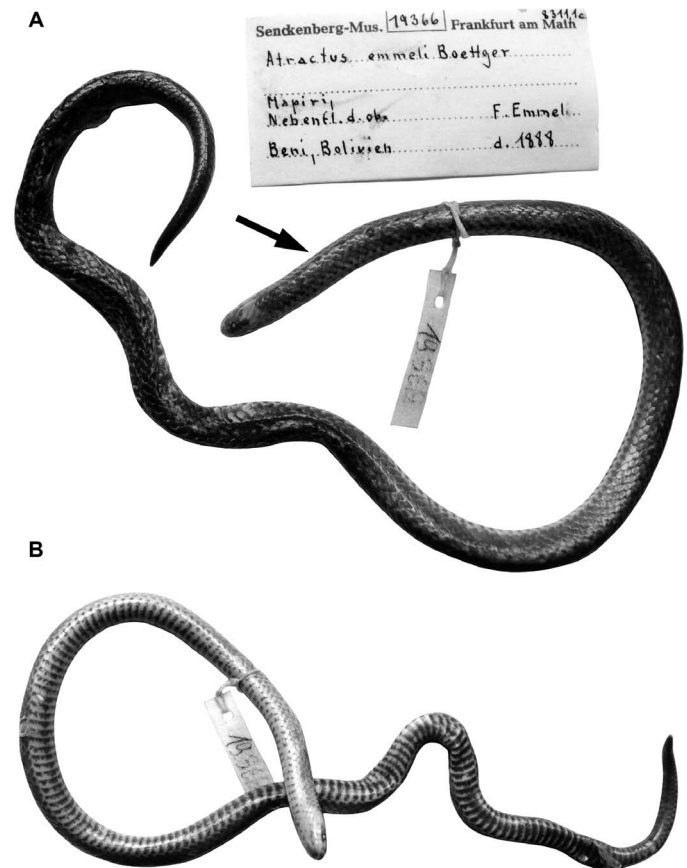

FIG. 4.—Dorsal (A) and ventral (B) views of body of *Atractus emmeli* (SMF 19366, paralectotype, snout–vent length 300 mm, caudal length 32 mm) from Mapiri River, Department of Beni, Bolivia.

demonstrate that populations differ in the frequency of distribution for some characters, most of these are actually polymorphic and cannot accurately delimit any species previously recognized in the *Atractus emmeli* complex. For these reasons, the qualitative and quantitative analyses are congruent in suggesting that *A. boettgeri, A. emmeli, A. paravertebralis* and *A. taeniatus* are conspecific. Based on these results, we propose herein formally to place *A. boettgeri, A. paravertebralis* and *A. taeniatus* in the synonymy of *A. emmeli*.

Although the Mato Grosso population was not discriminated in our morphometric analyses, this cluster differs from all other samples attributable to the *Atractus emmeli* complex in having 170–176 ventrals in males and 178–192 in females (vs. 151–165 in males and 167–185 in females of *A. emmeli*); hemipenis moderately bilobed and centrolinearly oriented with shallow spinulate calyces, well-defined capitular groove, and narrow sulcus spermaticus (vs. organ with slightly bilobed and centrifugally oriented lobes covered with well-developed spinulate calyces, comprising deep projections, indistinct capitular groove, and laterally expanded sulcus spermaticus in *A. emmeli*). In fact, the hemipenes of the Mato Grosso specimens are more similar to those of the parapatric *A. albuquerquei* than to those in other populations

←

Yungas, La Paz–Cochabamba Department boundaries, Bolivia; and *A. taeniatus* (D; CM 117, holotype, adult male, HL 9.1 mm) from Santa Cruz de la Sierra, Department of Santa Cruz, Bolivia.

Fig. 5.—Color pattern of specimens in the *Atractus emmeli* complex based on Bolivian sample from Guayaramerin (10°48′S, 65°22′W, 150 m), Department of Beni (A, USNM 123972, adult male, snout–vent length [SVL] 204 mm, caudal length [CL] 23 mm; B, USNM 123971, adult male, SVL 214 mm, CL 27 mm).

of *A. emmeli* (see below for additional comparisons between *A. albuquerquei* and Mato Grosso population).

On the other hand, the niche modeling entirely corroborates the results of the qualitative analysis of phenotypic characters, suggesting that the potential distribution model for *Atractus emmeli* does not include the available records of the Mato Grosso population, as well as the suitable environment

for occurrence of *A. albuquerquei* (Fig. 12; Fig. S2 in the Supplemental Materials available online). By contrast, comparing *A. albuquerquei* with specimens from the Mato Grosso population (in parenthesis), they also differ in having six supralabials and six infralabials, first three infralabials in contact with chinshields, three gular scale rows, three preventrals, 27–39 subcaudals in females and 37–44 in males,
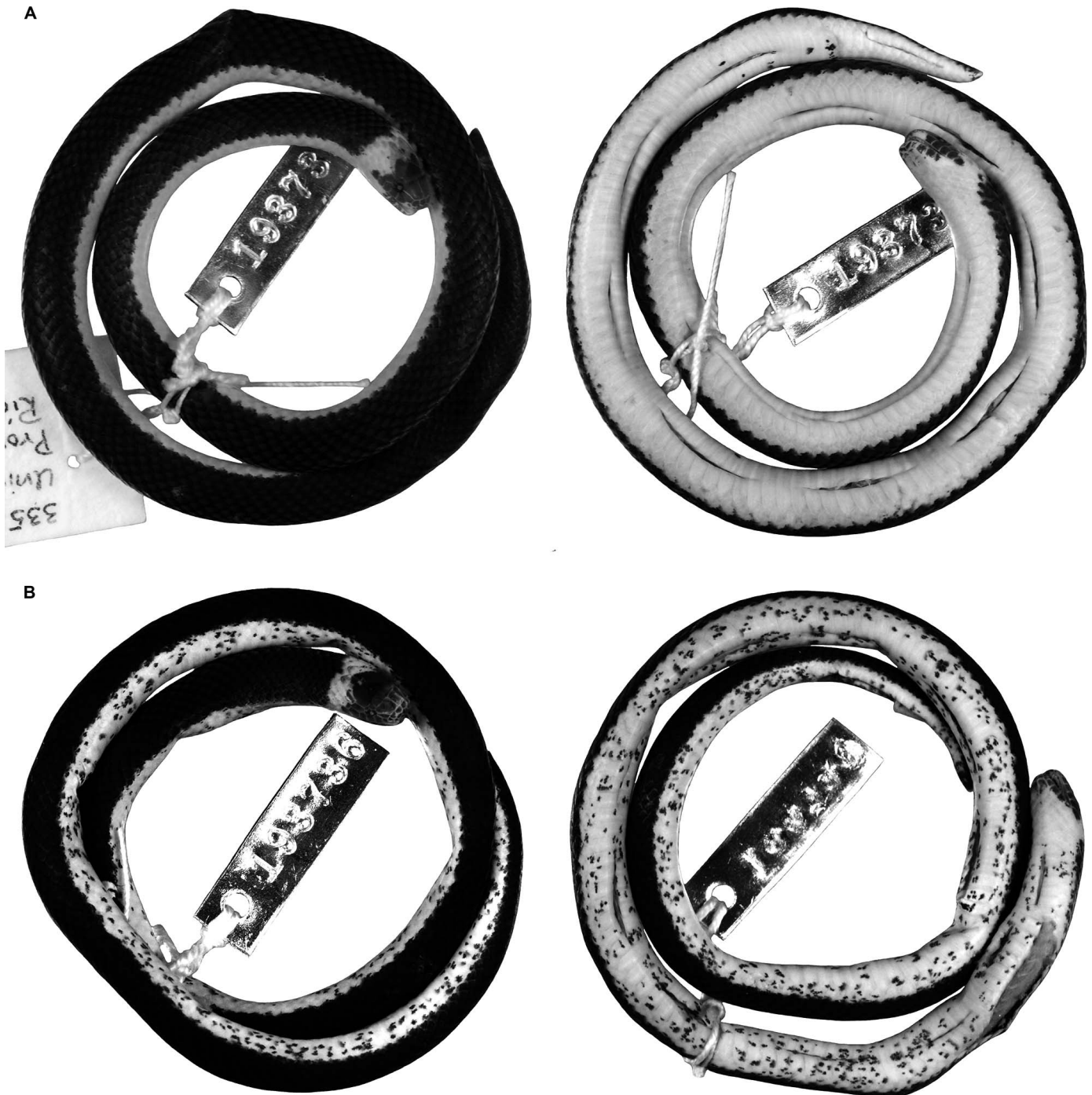
Fig. 6.—Color pattern of specimens in the *Atractus emmeli* complex based on Peruvian sample from Huallaga River, Universidad Agraria de la Selva (09°18′S, 75°59′W, 670 m), Tingo María, pronvince of Leoncio Prado, Department Huánuco (A, USNM 193736, adult male, snout–vent length [SVL] 231 mm, caudal length [CL] 23 mm; B, USNM 193739, subadult female, SVL 246 mm, CL 14 mm).

10–12% CL/SVL in females and 14.1–16.2% in males, and belly uniformly creamish white (vs. seven supralabials and infralabials, first four infralabials contacting chinshields, usually four gular scale rows and preventrals, 20–23 subcaudals in females and 25–28 in males, 7.4–9.3% CL/SVL in females and 9.7–12.3% in males, and belly creamish white with scattered black dots, blotches or mostly black).

Therefore, based on the compelling evidence from independent sources of phenotypic character systems (meristic, color pattern, and hemipenial morphology) in consonance with differences in the niche modeling, we propose here to recognize the Brazilian populations from the Parecis Plateau in the state of Mata Grosso as a new species described below.

Species Accounts
Atractus emmeli (Boettger 1888)
(Figs. 2–7, 9–10)

Geophis emmeli Boettger 1888:192. Two syntypes (SMF 19364 and 19366; Figs. 2A–B, 3A–B and 4) from

Fɪɢ. 7.—Color pattern of specimens in the *Atractus emmeli* complex based on Peruvian sample from la Pampa del Sacramento (08°00′S, 75°50′W), Castilian, Ucayali (A, ZFMK 41476, male, TL 225 mm; B, ZFMK 41477, male, TL 245 mm).

"Mapiri River," Department of Beni, Bolivia; Mertens (1967) designated SMF 19364 (Juvenile male) as lectotype.

Atractus emmeli (Boettger): [Transferred to *Geophis* by Boulenger 1894:311]; Boulenger 1896:645; Passos et al. 2018a illustrated the lectotype Fig. 1B.

Atractus boettgeri Boulenger 1896:645. Holotype BMNH 1946.16.29 (Adult female; Figs. 2B, 3C) from "Yungas" Bolivia. [**New synonymy**]

Atractus balzani Boulenger 1898:129. Holotype MSNG 28873 (Adult male) from "Missiones Mosetenes"; Passos et al. (2018a:fig 1A).

Atractus taeniatus Griffin 1916:173. Holotype CM 117 (Adult male; Figs. 2D, 3D) from Santa Cruz de la Sierra, Department of Santa Cruz, Bolivia. [**New synonymy**]

Atractus occipitoalbus: Fugler and Cabot 1995:45; Quintero-Muñoz 2013:76.

Atractus paravertebralis Henle and Ehrl 1991:160. Holotype ZFMK 39705 (Adult female; Figs. 2C, 3B), from "Baja Tambopada" (= lower Tambopata River), SW Puerto Maldonado, Department of Madre de Dios, Peru. [**New synonymy**]

Diagnosis.—*Atractus emmeli* can be distinguished from all congeners by the following combination of characters: (1) smooth dorsal scale rows usually 15/15/15, lacking apical pits; (2) postoculars two; (3) loreal moderately long; (4) temporal formula 1+2; (5) supralabials six to seven, third and fourth contacting orbit; (6) infralabials usually seven, first four scales in contact with chin shields; (7) maxillary teeth six to eight with posterior-most two teeth reduced in size; (8) gular
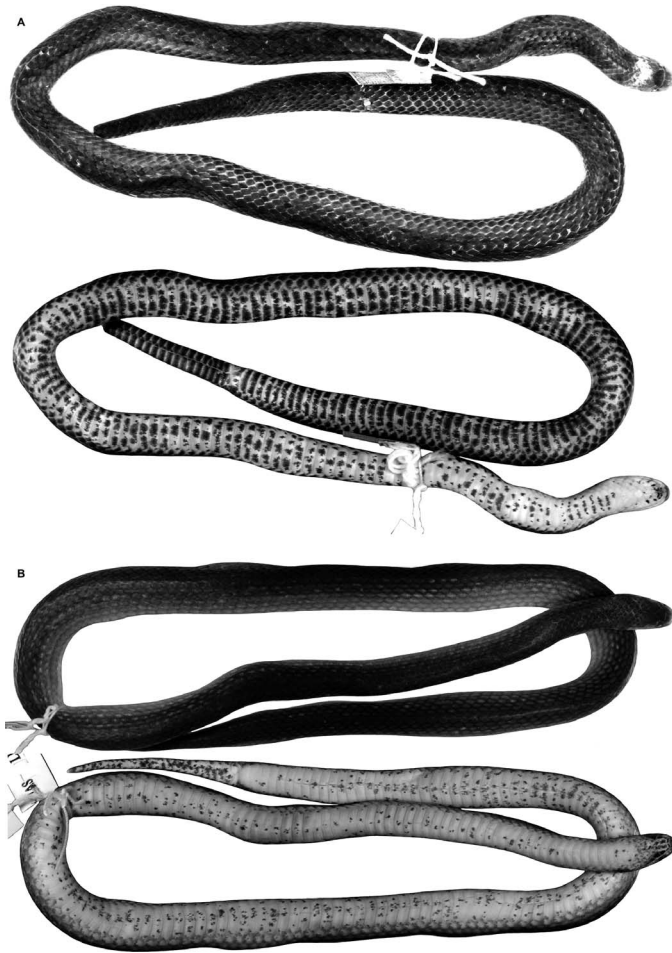
Fig. 8.—Color pattern of specimens in the *Atractus emmeli* complex based on Brazilian sample from hydroelectric center at Bocaiúva, Craveri River, Brasnorte, state of Mato Grosso (A, MNRJ 26734, holotype, adult male, snout–vent length [SVL] 296 mm, caudal length [CL] 42+N mm; B, UFMT 8138, paratype, adult male, SVL 285 mm, CL 35 mm).

scales in four series; (9) usually four preventrals; (10) ventrals in females 154–187, in males 147–169; (11) subcaudals in females 14–25, in males 20–31; (12) after preservation, dorsum of body light to dark brown or uniformly black, frequently with a broad white to pale brown parietal band most conspicuous in immature specimens, and occasionally (in the cases of lighter ground color) with irregular black blotches on paravertebral region; (13) after preservation, ventral surface of body and tail cream, usually heavily covered with variable black dots or spots, longitudinally along the midline of each ventral, laterally restricted to the anterior margins of each scale, irregularly distributed on venter or almost entirely darkening the belly and tail; (14) body size moderate, females reaching 382 mm, males reaching 304 mm SVL; (15) tail short in females (5.7–9.6% SVL), moderately long in males (9.2–14.7% SVL); (16) hemipenis moderately bilobed, semicapitated, and semicalyculated.

Comparisons.—Among all congeners, *Atractus emmeli* shares only with *A. albuquerquei* Cunha and Nascimento 1983, *A. caete* Passos, Fernandes, Bérnils and Moura-Leite 2010 and *A. reticulatus* the following combination of morphological characters: smooth dorsal scale rows 15/15/

15; frontal shield broader than long; nostril longer than prenasal; maxillary bone with a well-developed lateral process and no projection at the level of the last teeth; maxillary teeth 6–8; hemipenis moderately bilobed, semi-capitate, and semicalyculate; and dorsal ground color brown to uniformly black (see Discussion). *Atractus emmeli* differs from *A. albuquerquei* and *A. reticulatus* by usually having a conspicuous pale parietal band, belly frequently heavily pigmented with black marks, usually seven upper and lower labial scales, absence of naked pocket on the hemipenis, and 154–187 ventrals in females and 147–169 in males, 14–25 subcaudals in females and 20–31 in males (vs. absence of parietal band, venter frequently uniformly cream, usually six upper and lower labial scales, presence of naked pocket on the proximal region of hemipenis, and 192–211 ventrals in females and 170–184 in males, 27–38 subcaudals in females and 37–44 in males of *A. albuquerquei;* and venter uniformly cream, infralabials, 27–38 subcaudals in females and 37–44 in males of *A. reticulatus*). *Atractus emmeli* differs from *A. caete* by having four gular scale rows and conspicuous parietal band (vs. three gular scale rows and absence of parietal band).

Atractus emmeli also differs from the Amazonian species *A. occipitoalbus,* with which it was previously confused (see Remarks), by having nostril usually longer than prenasal, six to seven suparalabials, two postoculars, tail in females 5.7–9.4% SVL in males, 9.2–14.7% SVL, hemipenis with capitular groove barely defined on the asulcate side (vs. nostril shorter than prenasal, usually eight supralabials, usually single postocular in females, tail with 4.4–6.9% SVL in females and 9.6–14.1% in males, and hemipenis with capitular groove indistinct on the asulcate side of hemipenis). *Atractus emmeli* differs from all valid congeners with vouchered records in Bolivia (i.e., *A. bocki* Werner 1909, *A. latifrons* Günther 1868, *A. major* Boulenger 1893, *A. snethlageae* Cunha and Nacimento 1983, and *A. torquatus* Duméril, Bibron, and Dumeril 1854) by having usually 15/15/15 dorsal scale rows and dorsal ground color brown to uniformly black (vs. 17/17/17 and coloration variable but never brown to uniformly black).

Description.—Head barely distinct from body, about twice as long as wide, flattened in lateral view in adult specimens and slightly concave in juveniles; snout rounded in dorsal view and very truncated in lateral view; canthus rostralis indistinct; rostral subtriangular in frontal view, broader than high, slightly visible in dorsal view; internasal slightly wider than long; internasal suture sinister with respect to prefrontal suture; prefrontal slightly longer than wide; frontal pyramidal with posterior margin straight or barely projected on midline, slightly wider than long; supraocular subrectangular, about twice as long as wide; parietal twice as long as wide; nasal divided; nostril between prenasal and postnasal, usually longer than prenasal; prenasal about twice as high as long, similar in height to postnasal; postnasal about as high as long; loreal moderately long, contacting second and third supralabials; pupil round to subelliptical; postoculars subequals in high and length, eventually upper postocular slightly longer than lower; temporal formulae 1+2; anterior temporal twice as long as high; upper posterior fused or separated in two scales, when fused, forming a shield with about four times as long as wide; supralabials six or seven, third and fourth contacting eye;

FIG. 9.—General view in life of *Atractus emmeli* (collected by not traced after preservation on the respective collections) from the Samuel Hydroelectric Power Plant (08°45′S, 63°54′W, 90 m), Porto Velho, state of Rondônia, Brazil (A–D) and from the Los Lagos Lodge (12°46′S, 65°48′W, 145 m), Department of Beni, Bolivia (E–F). Photos by Systema Naturae Ltda (A–D) and M. Jansen (E–F). A color version of this figure is available online.

second supralabial higher than first and with similar height of third supralabial; generally sixth scale taller and seventh scale longer than remaining supralabials; fifth supralabial taller and longer when fused to fourth supralabial; symphysial semicircular, about four and five times broader than long, separated from chinshields by first pair of infralabials; symphysial rarely contacting chinshields; seven infralabials, first four contacting chinshields; chinshields about three times longer than wide; gular scale rows usually four; usually four preventrals; dorsal scale rows usually 15/15/15, scales smooth, lacking apical pits and supracloacal tubercles; caudal spine longer than last subcaudal, robust, conical and acuminated. Maxillary bone dorsally arched in its anterior portion and posterior region projected downward; maxilla with lateral process of maxilla well-developed and not projecting posteriorly to the level of last two maxillary teeth;

maxilla with six to eight, but usually seven teeth; teeth angular in cross-section, robust at base, narrower at apices, curved posteriorly; first tooth smaller and close to second; third to fifth teeth large, moderately spaced, similar in size; last two teeth gradually reduced in size and more closed located; last two teeth smaller and less spaced than the anterior teeth (Fig. 3).

Color pattern in preservative.—Dorsum of head brown to black, except for broad parietal light band (white to pale brown) usually present; eventually, parietal band reduced in size and/or darkened and, most rarely, entirely obscured in melanic specimens; dorsal and lateral portions of snout and occipital region sometimes light brown, with frontal shield and eye region darkened (black); usually pale band arising on anterior to midportion of parietal shields, extending to the end of parietals and upper posterior temporals or reaching first dorsal scale rows; laterally, head brown or black up to level of lateral extension of pale band posteriorly, giving impression of conspicuous black cephalic-cap separated from the body by conspicuous occipital collar (= pale parietal band); lateral head black generally extending to ventral margins of supralabials; occasionally black pigmentation restricted to dorsal edges or midportion of supralabials; some specimens with anterior scales (first two and anterior portion of third supralabials, nasals, and anterior region of loreal) light brown and with dark brown supralabials in contact with eye (posterior region of third, fourth, fifth, and anterior portion of sixth and seventh supralabials); symphysial, infralabials, and chinshields frequently mostly dark brown to black or with cream background heavily marked with black blotches; sometimes gular region predominantly cream with few dark marks concentrated at the level of the eye, covering dorsal portion of third to fifth infralabials, symphysial and anterior region of chinshields; occasionally, gular region almost entirely cream with few scattered dark spots; venter generally cream with irregular dots, spots, or blotches, which may cover entire belly; dark pigmentation sometimes concentrated on anterior or median regions (or both), restricting cream parts to posterior and lateral regions of each ventral scale; frequently venter cream poorly to heavily scattered with nearly rounded spots or blotches; most rarely belly almost entirely cream with few dispersed black spots or entirely dark brown to black without any cream marks; ventral surface of tail cream with darker pigmentation concentrated on midline or posterior region of subcaudals along sutures among scales; tail mostly dark brown to black eventually, except for anterior cream margins or entirely black; dorsal ground color of body brown to black, except for central portion of first dorsal scale rows generally lighter (cream to beige); eventually dorsum light brown to medium brown with paired (or irregular) paravertebral rounded black spots or blotches (one to two scales long); most rarely presence of barely defined irregular vertebral line occasionally laterally connected to paravertebral marks. In juvenile specimens the light parietal band is very conspicuous and contrasting with darker ground color of body, which is sometimes obscured by dark pigment in adult individuals (Figs. 2–7).

Color pattern in life.—Dorsum of head black except for a white, yellow, or light brown parietal band; head in lateral view mostly black, with yellow spots on supralabials and infralabials; posterior supralabials and temporals above
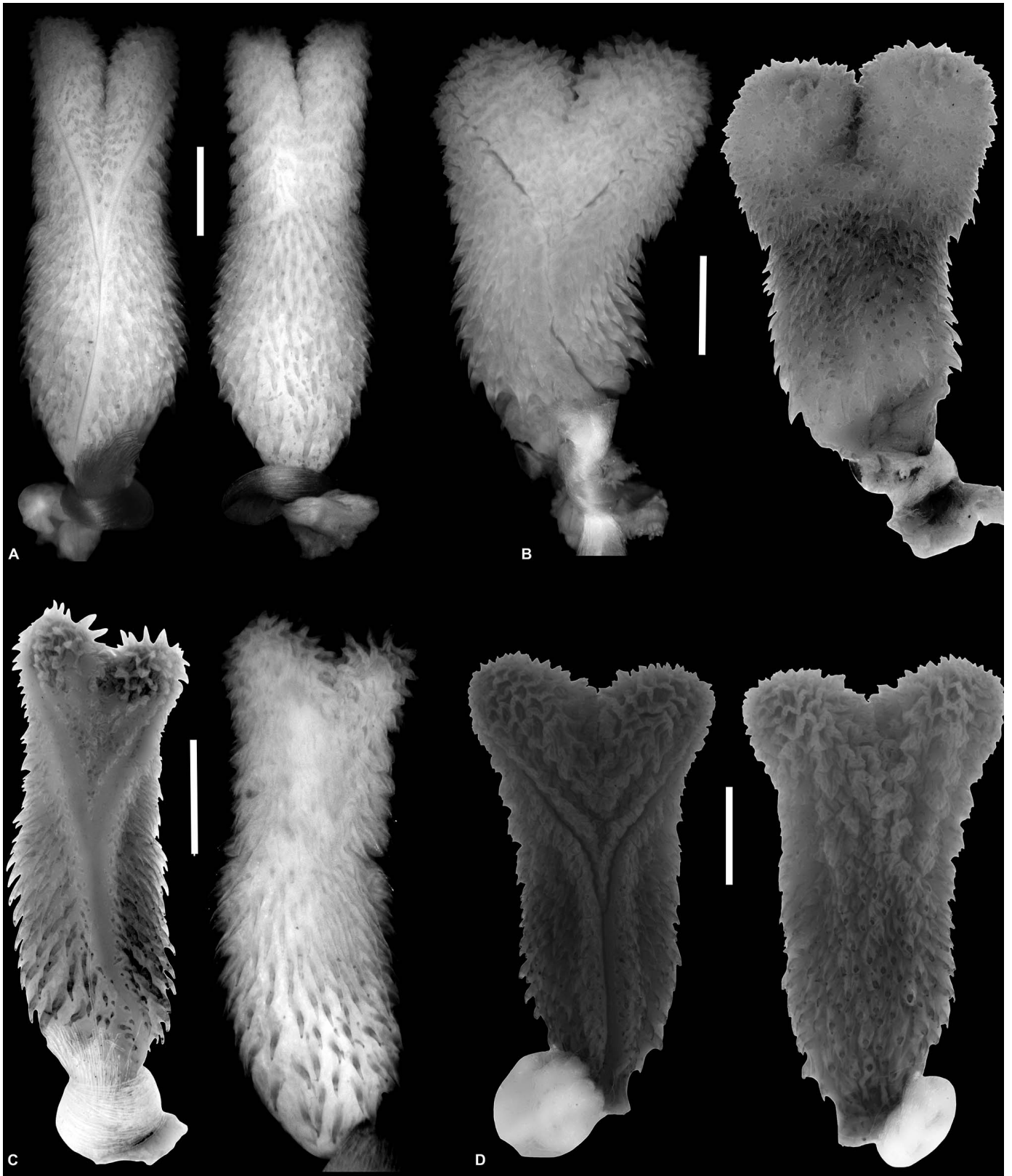
Fig. 11.—Hemipenial morphology in the *Atractus emmeli* complex, displaying the sulcate (left) and asulcate (right) face of the organs from the specimens collected at Craveri River (A–B, MNRJ 26734 and UFMT 8138), Brasnorte, Mato Grosso, Brazil; Guayaramerin (C; USNM 123971), Yacuma, Beni, Bolivia; and Coronel Portillo (D; USNM 193736), Pucallpa, Loreto, Peru. Scale = 5 mm.

occipital region white, yellow, or brown according to tone of the parietal light band; dorsum of body uniformly black; ventral surface of body and tail creamish red to pinkish; sometimes reddish or pinkish pigment concentrated on paraventral region, covering lateral portions of ventrals and central portion of first dorsal scale rows, and lighter portions of subcaudals (Figs. 9–10).

Hemipenial variation (*n* = 6).—Organs in situ (retracted) extend to level of seventh to eighth (*n* = 3) subcaudal and bifurcate at level of sixth (*n* = 2) to seventh subcaudal (*n* = 1). Fully everted and maximally expanded hemipenes moderately bilobed, semicapitate, and semicalyculate; lobular region similar (USNM 193736) or wider than hemipenial body (USNM 123931); lobes clavate with rounded tips (USNM 123931, 193736); lobes almost symmetrical, but right lobe usually slightly longer than left; lobes centrolinearly (USNM 193736) or centrifugally (USNM 123931) oriented; lobes uniformly covered with spinulate calyces on both sides of hemipenis; calyces on distal region of lobes ornamented with high concentration of spines (USNM 193736) or spinules projected upward (USNM 123931); spinules; basal and lateral regions of capitulum with diagonal flounces apparently originated from connection of horizontal walls of calyces but lacking their vertical walls (USNM 193736); high concentration calyces sometimes with increased thickness and very irregular connections (USNM 123931); calyculated flounces more conspicuous on lateral region and asulcate side of hemipenis; occasionally, high concentration of deep calyces on asulcate side of organ generates median and lobular crests (USNM 123931); sometimes hemipenis with asulcate side densely concentrated with calyces lacking flounces and crests (USNM 192736); intrasulcar region of capitulum densely covered with irregular spinulate calyces; capitular groove barely distinct (USNM 123931) or slightly marked (USNM 123931) on asulcate side and less evident on sulcate side of hemipenis; capitulum varying from 40 to 50% length of hemipenial body; hemipenial body elliptical and scattered with large
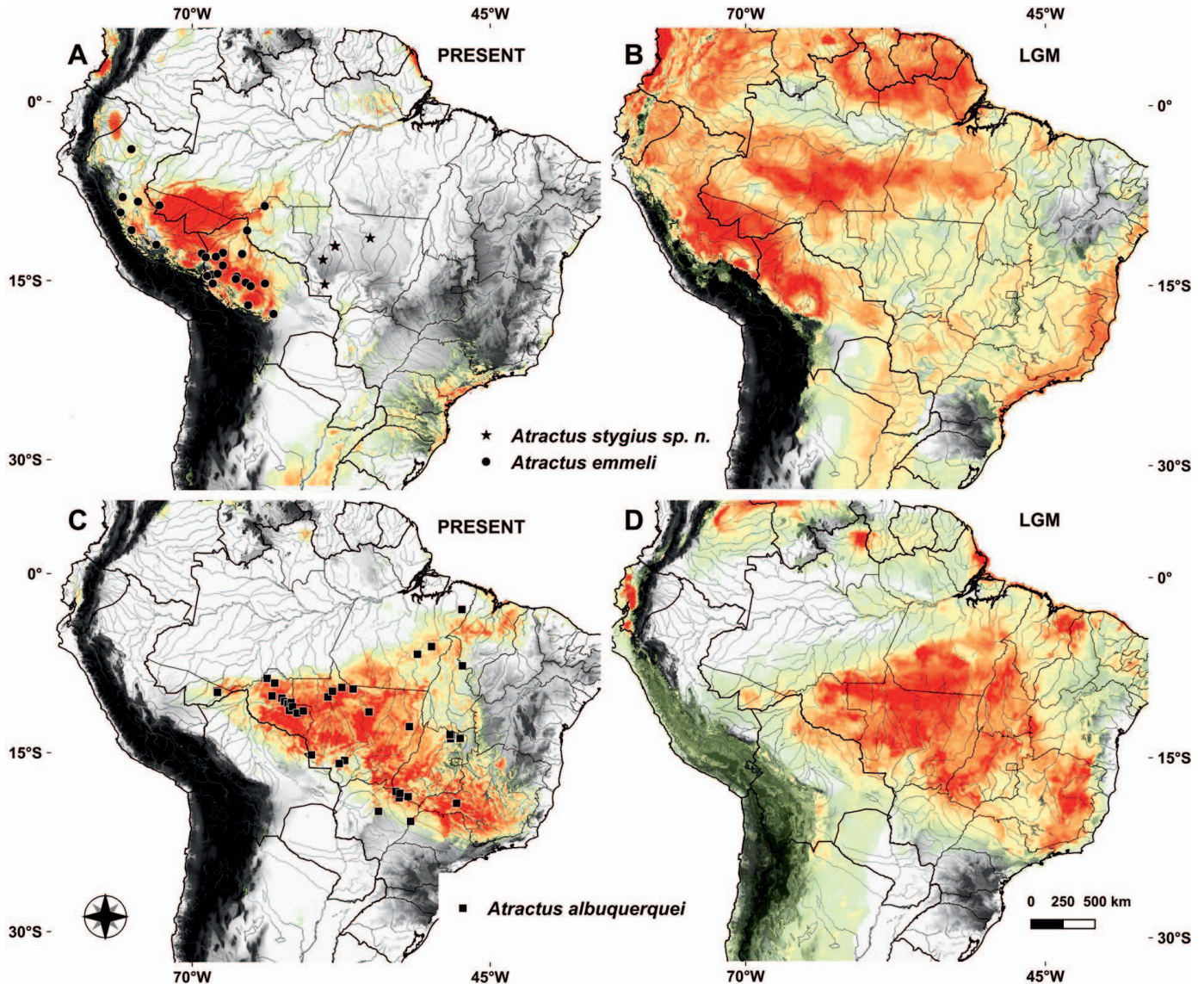

FIG. 12.—Synthesis of the niche models at present time (A) and based on Last Glacial Maximum (about 22,000 years ago; Community Climate System Model 4; Braconnot et al. 2007), to *Atractus emmeli* and *A. stygius* (B), and to *A. albuquerquei* at present time (C) and on Last Glacial Maximum (D).

hooked spines; hemipenial body densely covered with spines without nude areas; larger spines generally located laterally below sulcus spermaticus bifurcation; sulcus bifurcates for about half of organ with each branch centrifugally oriented, running to tip of lobes; sulcus spermaticus margins expanded (USNM 123931, 193736); sulcus spermaticus bordered by spinules from base of organ to apices of lobes; basal naked pocket absent or indistinct; most basal region of hemipenis without spines and with longitudinal plicae and dispersed spinules (Fig. 11C–D).

Meristic and morphometric variation.—Largest male 304 mm SVL, 31 mm CL; largest female 382 mm SVL, 31 mm CL; tail 9.2–14.7% SVL (mean = 11.2; SD = 1.3; n = 24) in males, 5.7–9.6% SVL (mean = 7.7; SD = 1.1; n = 25) in females; ventrals 147–169 (mean = 156; SD = 6.7; n = 24) in males, 154–187 (mean = 170.2; SD = 9.9; n = 28) in females; subcaudals in males 20–31 (mean = 24.3; SD = 2.6; n = 25) in females 14–25 (mean = 19.5; SD = 3.6; n = 27); supralabials 5 (n = 1 side), 6 (n = 16 sides), 7 (n = 67 sides), or 8 (n = 1 side); infralabials 7 (n = 103) or 8 (n = 3); gular scale rows 3 (n = 4 sides) or 4 (n = 56 sides); dorsal scale rows 15/15/15 (n = 50), 15/17/17 (n = 1), or 17/17/17 (n = 2); dorsal scale rows at level of second subcaudal 6–9 (mean = 7.9; SD = 0.6; n = 72 sides); midbody diameter 3.0–7.4 mm (mean = 5.1; SD = 1.2; n = 22); maxillary teeth 6 (n = 11 sides), 7 (n = 55 sides), or 8 (n = 3 sides); palatine teeth 5 (n = 3 sides). One specimen (MUSM 2313) displayed the first pair of infralabials reduced, allowing contact between symphysial and chinshields.

Distribution.—Amazonian rainforest from the eastern slopes of the Andes to Brazilian portions of Amazonia, from Yungas mountain range (ca. 16°20′S, 66°45′W) in Department of Cochabamba, Bolivia, northwest to Coronel Portillo (03°15′S, 76°55′W) in Department of Loreto, Peru, and southeast to Porto Velho (08°45′S, 63°54′W) in state of Rondônia, Brazil. *Atractus emmeli* occurs in lowland rainforest, Beni savannas to submontane forest between 90 and 1000 m elevation (Fig. 13).

Remarks.—Although the records of *Atractus occipitoalbus* in the Bolivian (Fugler 1983 and 1984 in Fugler and Cabot 1995; Fugler and De la Riva 1990) and Peruvian (Carrillo and Icochea 1995; Lehr 2002) snake fauna are not new, Henle and Ehrl (1991) and Quinteros-Muñoz (2013) were the only studies in which voucher specimen were mentioned. Passos et al. (2010a) reviewed the taxonomy of the *A. occipitoalbus* species complex and included only Colombia and Ecuador in their range maps. We examined the photos and data from the specimens reported by Henle and Ehrl (1991; ZFMK 41476–77; see our Fig. 7), as well as the data and images provided by Quintero-Muñoz (2013:76, and their figs. 1–2) previously identified as new records of *A. occipitoalbus* from Peru and Bolivia, respectively. On the basis of the available evidence, we re-identify all these individuals as *A. emmeli* (see comparisons of diagnostic characters between aforementioned species). Therefore, *A. occipitoalbus* must be excluded from the snake fauna of Bolivia. Additionally, two Peruvian specimens (MUSM 2313 from unknown provenance and MUSM 27402 from Trompeteros, 03°48′S, 75°03′W, ca. 130 m, Department of Loreto) have 17/17/17 and 15/17/17 dorsal scale rows, respectively. However, all remaining characters of these individuals agree with *A. emmeli* and, therefore, we consider

both to be anomalous with respect to the number of dorsal scale rows (see Passos et al. 2018c for detailed explanation). Boulenger (1896:645) reported the specimen "a" of *A. emmeli* collected by Emilio Goeldi. We examined high-resolution images of this individual (Fig. S3 in the Supplemental Materials available online) and confirm its identification as *A. emmeli,* even though there are no additional records for this species from the state of Pará, Brazil.

*Atractus **stygius** sp. nov.*
(Figs. 8, 14)

Atractus albuquerquei Zaher et al. 2005:32 (in part) [Possible misidentification: MZUSP 11157, 11242].

Holotype.—Adult male, MNRJ 26734 (formerly UFMT 8139), collected in 2009 by Universidade Federal de Mato Grosso team during the faunal rescue operation for the construction of a small hydroelectric plant at Bocaiúva (12°29′50″S, 57°52′30″W; ca. 312 m), Craveri River, municipality of Brasnorte, state of Mato Grosso, Brazil.

Paratypes.—Nine specimens, all from the state of Mato Grosso, Brazil: UFMT 8137 (adult female), UFMT 8138 (adult male), UFMT 8140 (juvenile female), UFMT 8141 (juvenile male), UFMT 8142 (juvenile male) same data as the holotype; an adult female, UFMT 3949, collected by M. Carvalho on May 2004, specimen found in the stomach of a *Pseudoboa coronata* (UFMT 3726), from Continental Farm (11°30′06″S, 55°12′18″W; ca. 350 m), municipality of Claudia; an adult female, MNRJ 26735 (formerly UFMT 9024), collected by R. Ávila and R. Kawashita-Ribeiro on 18 January 2011 at Vale de São Domingos (14°57′05″S, 59°10′06″W; ca. 500 m), municipality of Jaurú; a juvenile female, UFMT 9116, collected on 3 March 2011 by R. Kawashita-Ribeiro at Jurena River, São Nicolau Farm (09°51′S, 58°14′W; ca. 220 m); an adult female, MZUSP 20667, collected on 17 October 2012 by JGP Consultoria Ambiental team in the faunal rescue operation for the construction of a small hydroelectric plant at Segredo (13°13′22″S, 59°01′36″W; ca. 500 m), Juruena River, municipality of Sapezal.

Diagnosis.—*Atractus stygius* can be distinguished from all congeners by the following combination of characters: (1) smooth dorsal scale rows 15/15/15; (2) postoculars two; (3) loreal moderately long; (4) temporal formula usually 1+2; (5) supralabials seven, third, and fourth contacting eye; (6) infralabials seven, first four contacting chinshields; (7) maxillary teeth seven; (8) gular scale rows usually four; (9) preventrals usually four; (10) ventrals 178–192 in females, 170–176 in males; (11) subcaudals 20–23 in females, 25–28 in males; (12) in preservative, dorsum dark brown to black except for a conspicuous pale brown to beige parietal band; (13) in preservative, ventral surface of body cream, heavily pigmented with black marks, to mostly black; (14) maximum body size moderate in females (470 mm SVL) and males (390 mm SVL); (15) tail size small in females (8.0–9.7% SVL) and in males (8.1–10.4% SVL); (16) hemipenis moderately bilobed, semicapitate, and semicalyculate.

Comparisons.—Among all congeners, *Atractus stygius* shares only with *A. albuquerquei, A. caete, A. emmeli,* and *A. reticulatus* the following combination of morphological characters: dorsal scales smooth, rows 15/15/15; frontal
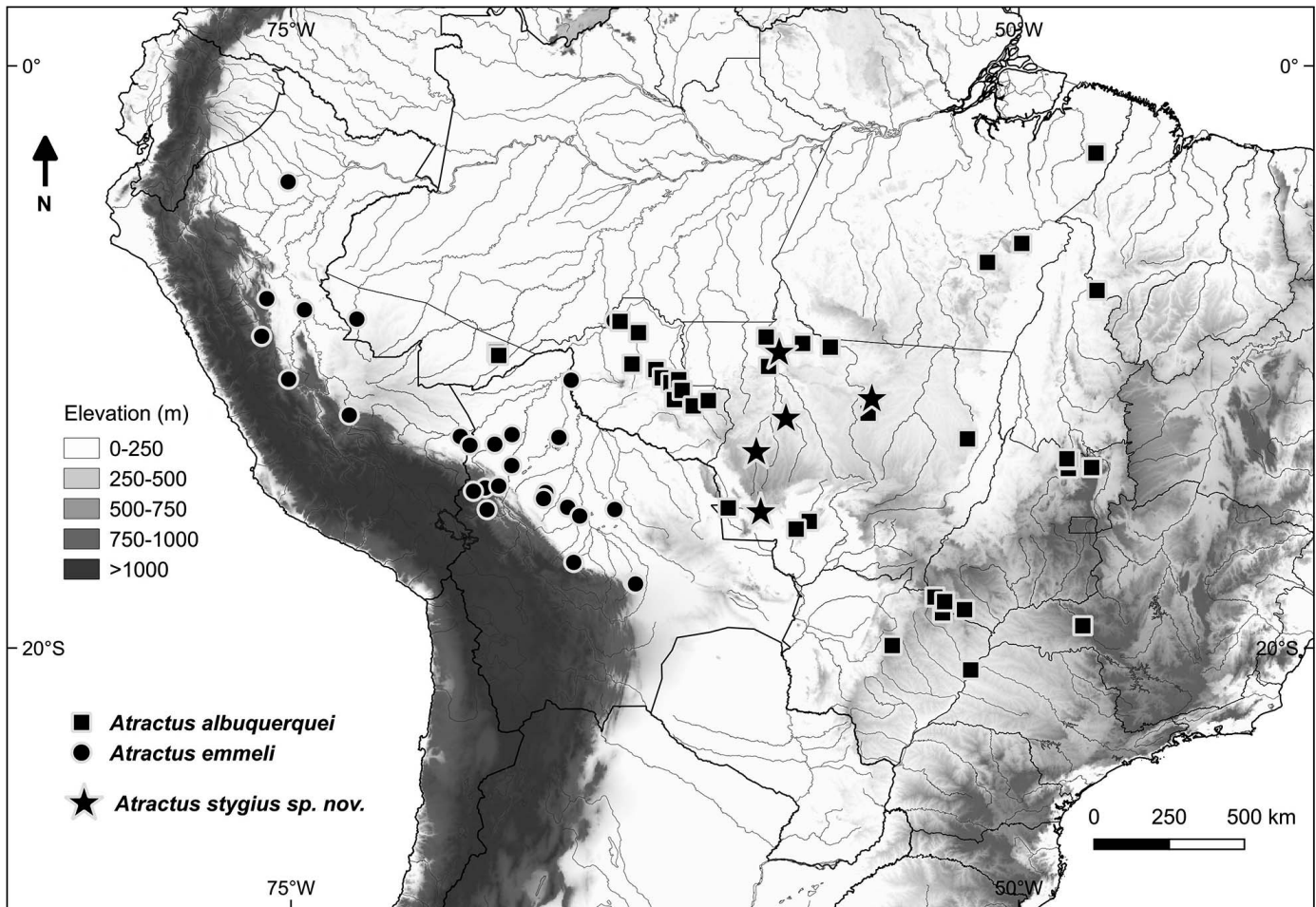
Fig. 13.—Known distribution of *Atractus albuquerquei, A. emmeli,* and *A. stygius*.

shield broader than long; nostril longer than prenasal; maxillary bone with a well-developed lateral process and no projection at the level of the last teeth; maxillary teeth six to eight; hemipenis moderately bilobed, semicapitate, and semicalyculate; dorsum ground color dark brown to uniformly black (see Discussion). *Atractus stygius* differs from *A. albuquerquei* and *A. reticulatus* by having a conspicuous pale parietal band in adult specimens, belly frequently heavily pigmented with black marks, usually seven upper and lower labial scales, absence of naked pocket on hemipenis, and 170–176 ventrals in males and 178–192 in females, 20–23 subcaudals in females and 25–28 in males (vs. absence of parietal band in adult specimens [in *A. reticulatus*], venter frequently uniformly cream, usually six upper and lower labial scales, presence of naked pocket on the proximal region of hemipenis, and 192–211 ventrals in females and 170–184 in males, 27–38 subcaudals in females and 37–44 in males of *A. albuquerquei;* and venter uniformly cream, infralabials, 27–38 subcaudals in females and 37–44 in males of *A. reticulatus*). *Atractus stygius* differs from *A. caete* by having four gular scale rows and conspicuous parietal band (vs. three gular scale rows and absence of parietal band). *Atractus stygius* differs from *A. emmeli* in having 170–176 ventrals in males and 178–192 in females; CL/SVL 8.1–10.4% in males, 8.0–9.7% in females; hemipenis moderately bilobed and centrolinearly oriented with shallow spinulate

calyces, well-defined capitular groove, and narrow sulcus spermaticus (vs. 147–169 in males and 154–187 in females; CL/SVL 9.2–14.7 in males, 5.7–9.6% in females; organ with slightly bilobed and centrifugally oriented lobes covered with huge developed spinulate calyces, comprising deep projections, indistinct capitular groove, and laterally expanded sulcus spermaticus in *A. emmeli*).

Atractus stygius also differs from the other cis-Andean congeners with 15/15/15 dorsal scale rows, except *A. occipitoalbus* Jan 1862 and *A. orcesi* Savage 1955, by dorsum uniformly black in preservative (vs. dorsum in preservative cream to light brown with dark marks but never uniformly black in *A. boimirim* Passos, Prudente, and Lynch 2016; *A. edioi* Silva, Silva, Ribeiro, Souza, and Souza 2005; *A. insipidus* Roze 1961; *A. paraguayensis* Werner 1924; *A. potschi* Fernandes 1995; *A. punctiventris* Amaral 1933; *A. tartarus* Passos, Prudente, and Lynch 2016; or black with conspicuous paired white dots in *A. avernus* Passos, Chiesse, Torres-Carvajal, and Savage 2010 or beige spots or blotches in *A. tamessari* Kok 2006). *Atractus stygius* differs from *A. occipitoalbus* and *A. orcesi* by having seven supralabials, two postoculars in females, and 170–176 ventrals in males and 178–192 in females and 25–28 in males, 20–23 subcaudals in females (vs. usually eight supralabials in both species; usually single postocular in females of *A. occipitoalbus;* 129–155 ventrals in males, 143–172 in females and
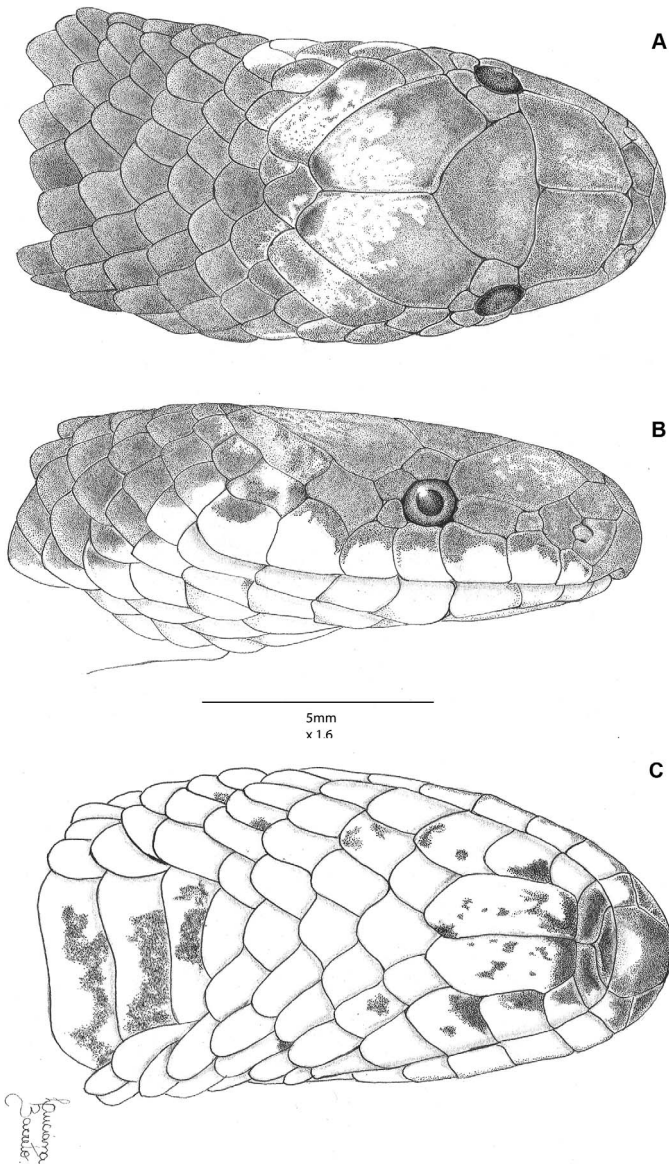
Fig. 14.—Dorsal (A), lateral (B), and ventral (C) views of head of the holotype of *Atractus stygius* from Craveri River, Brasnorte, Mato Grosso, Brazil.

20–26 subcaudals in males, 9–17 in females of *A. occipitoalbus;* and 134–152 ventrals in males, 142–158 in females and 18–34 subcaudals in males, 13–22 in females).

Description of the holotype.—Adult male, SVL 295 mm, CL 24 mm + *N* (tail partially amputated); head slightly distinct from body; head length 11.0 mm (3.7% SVL); head width 5.2 mm (47% head length); rostral–orbit distance 3.1 mm; nostril–orbit distance 2.2 mm; interorbital distance 3.7 mm; head flattened in lateral view; snout rounded in dorsal view, truncate in lateral view; canthus rostralis inconspicuous; rostral subtriangular in frontal view, 1.7 mm wide, 1.3 mm high, well-visible in dorsal view; internasal 1.0 mm long, 0.9 mm wide; internasal suture sinistral with respect to prefrontal suture; prefrontal 2.0 mm long, 2.1 mm wide; supraocular subtrapezoidal, 1.0 mm long, 0.7 mm wide at broadest point; frontal subpyramidal, 3.0 mm long, 2.3 mm wide; parietal 4.0 mm long, 2.2 mm wide; nasal entirely divided, nostril dividing prenasal from postnasal; prenasal 0.7 mm high, 0.5 mm long; postnasal 0.9 mm high, 0.6 mm long; loreal on right side anteriorly divided; left loreal 1.4 mm long, 0.5 mm high; second and third supralabials contacting loreal; eye diameter 1.0 mm; pupil rounded; two postoculars similar in height; upper postocular 0.5 mm long, 0.5 mm high; lower postocular slightly taller, 0.6 mm high; temporal formula 1+2; first temporal 1.5 mm long, 0.8 mm high; upper posterior temporals fused, 3.1 mm long, 0.7 mm wide; supralabials seven, third and fourth contacting eye; first supralabial taller and shorter (0.7 mm high × 0.6 mm long) than second (1.1 mm high and long); third supralabial similar in height and longer (1.1 mm) than second; sixth supralabial taller (1.2 mm) and seventh longer (1.4 mm) than remaining supralabials; symphysial subtriangular, 1.2 mm wide, 0.4 mm long; first pair of infralabials preventing symphysial–chinshields contact; infralabials seven, first four contacting chinshields; chinshields 2.7 mm long, 1.0 mm wide; gular scale rows three; preventral one; ventrals 176; subcaudals 18+n (tail incomplete); dorsal scale rows 15/15/15, lacking apical pits and supracloacal tubercles; midbody diameter 5.3 mm (1.8% SVL). Maxillary bone arched upward anteriorly in lateral view, ventral portion curved anteriorly and nearly flattened on median to posterior portion; maxillary teeth seven; teeth angular in cross-section, robust at base, narrower at apices, curved posteriorly; first two teeth smaller and closely spaced; third to fifth teeth large, moderately spaced, similar in size; last two teeth gradually reduced in size and widely spaced; maxillary diastema absent or indistinct from interspaces between fifth and sixth teeth; last two teeth smaller and less spaced than the anterior teeth; lateral process of maxilla well-developed (Fig. 14).

Dorsum of head dark brown with some pale brown diffuse dots covering prefrontals and frontal; dorsal background of head dark brown, extending to anterior portion of parietals; posterior region of parietals and adjacent temporals with a conspicuous light band creamish brown to pale brown; lateral sides of head uniformly dark brown above dorsal margins of supralabials, except for diffuse pale brown pigmentation covering prenasal and temporal region; most of supralabials, occipitals, and dorsal portions of infralabials uniformly creamish white; gular region mostly creamish white; symphysial, first pair of infralabials, and anterior portion of chinshields with concentrated dark brown spots; midposterior region of chinshields and anterolateral portions of second to fourth infralabials with irregular dark brown spots; remaining parts of gular region almost uniformly cream with a few bark brown dots; venter cream with irregular dark brown dots, spots, and blotches covering ventral scales; ventral dark pigmentation increasing in area and concentration toward posterior region of body; ventral scales on anterior third of body predominantly cream with dark brown marks; from midbody to posterior region of belly mostly dark brown with few irregular cream areas; ventral surface of tail cream with pale brown pigmentation concentrated on posterior sutures between subcaudals; dorsal ground color of body and tail almost uniformly dark brown; first dorsal scale row with light brown pigment on anterior portion of each scale (Figs. 8, 14).

Color pattern variation in preservative.—Dorsum of head dark brown to black from rostral to parietals; snout region occasionally with pale brown dots covering rostral,

internasals, loreal, and nasals anteriorly and temporals posteriorly; light pigments regularly or irregularly distributed above parietal and adjacent temporal region, but always forming a pale brown parietal band (one to two dorsal scales wide); parietal band more conspicuous and lighter (cream to creamish brown) in juvenile specimens; parietal pale band usually darkened and less conspicuous in adult specimens; lateral side of head with dark brown pigmentation reaching dorsal edges to dorsal half of supralabial; sometimes supralabials on the orbital region mostly brown, with dots reaching labial border of third and fourth supralabials; dark brown dots usually covering dorsal region of sixth and anterior region of seventh supralabial; posterior region of seventh supralabial usually uniformly creamish white; symphysial, infralabials, chinshields, and gular scale rows variable, but frequently with cream background and few scattered brown dots or spots concentrated anteriorly; brown marks concentrated above symphysial, first pair of infralabials, and posterior portions of remaining infralabials (on the suture with chinshields), and anterior third of chinshields; gular region occasionally dark brown; venter usually creamish white with small dark brown dots or spots concentrated on the center of each ventral scale; concentration of dark pigmentation increasing toward posterior region of body; occasionally, brown dots covering entire anterior surfaces of ventral scales; ventral surface of tail mostly dark brown with light pigmentation (beige to pale brown) usually restricted to posterior suture between paired subcaudals; tail occasionally mostly brown due to high concentration of dispersed brown dots or spots; dorsum of body almost uniformly dark brown to black.

Hemipenial morphology.—Organs in situ (retracted) extend to the level of eighth ($n = 2$) to ninth ($n = 4$) subcaudal and bifurcate at the level of seventh to eighth subcaudal ($n = 2$). Fully everted and maximally expanded hemipenes moderately bilobed, semicapitate, and semicalyculate; lobular region similar to (MNRJ 26734) or wider than hemipenial body (UFMT 8138); lobes clavate with rounded (UFMT 8138) or nearly flattened (MNRJ 26734) tips; lobes almost symmetrical, but right lobe usually slightly longer than left; lobes centrolinearly oriented (UFMT 8138, MNRJ 26734); lobes uniformly covered with spinulate calyces on both sides of hemipenis; calyces on distal region of lobes ornamented with spinules projected upward (UFMT 8138); spinules, occasionally, gradually replaced by papillae toward apices of lobes (MNRJ 26734); basal and lateral regions of capitulum with diagonal flounces apparently originated from connection of horizontal walls of calyces but lacking their vertical walls (MNRJ 26734); high concentration calyces sometimes with increased thickness and very irregular connections (UFMT 8138); calyculated flounces more conspicuous on lateral region and asulcate side of hemipenis; capitular groove slightly marked (UFMT 8138) or well-defined (MNRJ 26734) on asulcate side and less evident on sulcate side of hemipenis; capitulum varying from 40 to 50% length of hemipenial body; hemipenial body elliptical and with scattered large hooked spines; hemipenial body densely covered with spines without nude areas; larger spines generally located laterally below sulcus spermaticus bifurcation; sulcus spermaticus bifurcates for about half of organ with each branch centrifugally oriented, running to tip of lobes; sulcus spermaticus margins relatively narrow (UFMT 8138); sulcus spermaticus bordered by spinules from base of organ to apices of lobes; basal naked pocket absent or indistinct; most of basal region of hemipenis without spines and with longitudinal plicae and dispersed spinules (Fig. 11A–B).

Meristic and morphometric variation.—Largest male 270 mm SVL, 36 mm CL; largest female 390 mm SVL, 38 mm CL; tail 8.1.2–10.4% SVL (mean = 9.5, SD = 1.2, $n = 3$) in males, 7.4–9.7% (mean = 8.6, SD = 1.0, $n = 6$) in females; body diameter 3.0–7.4 (mean = 5.4, SD = 1.6, $n = 9$); ventrals 170–176 (mean = 173, SD = 2.5, $n = 5$) in males, 178–192 (mean = 182.2, SD = 6.8, $n = 5$) in females; subcaudals 26–28 (mean = 27.2, SD = 1.0, $n = 3$) in males, 20–26 (mean = 22.4, SD = 1.9, $n = 6$) in females; temporal formulae 1+2 ($n = 19$ sides) or 1+1 ($n = 1$ side); preventrals 3 ($n = 2$) or 4 ($n = 6$); dorsal scales rows at the level of second subcaudal 6–9 (mean = 7.9, SD = 0.9, $n = 20$ sides). The specimen UFMT 8137 has prefrontal entirely fused and UFMT 9116 shows a single postocular on the one side of head.

Etymology.—The specific epithet stygius is a Latin adjective meaning of hell or the underworld. The word is also used in reference to something pernicious or tragic. We employed this name because of the secretive habits of the new species as well as an urgent alert for the absurd levels of deforestation that the Cerrado savannas have suffered in recent years, as a result of the indiscriminate expansion of soybean monoculture (Boerema et al. 2016). This scenario is even more worrisome for the conservation agenda given the growing disregard of Brazilian authorities regarding the preservation of natural environments, and considering the previously undetected high levels of herpetofaunal endemism recently reported for the Cerrado (Nogueira et al. 2011; Azevedo et al. 2016; Guedes et al. 2017).

Distribution.—Parecis Plateau and adjacent areas of the Brazilian Shield, from São Nicolau Farm (09°51′19″S, 58°14′54″W) southeast to Claudia (11°30′06″S, 55°12′18″W), southwest to Brasnorte (12°29′50″S, 57°52′30″W), southwest to Sapezal (13°13′22″S, 59°01′36″W), and southwest to Jaurú (14°57′05″S, 59°10′06″W). *Atractus stygius* occurs mostly in the Cerrado ecoregion between 200 and 500 m elevation (Fig. 13).

<div align="center">DISCUSSION</div>

As previously pointed out by McCoy (1971), samples attributed to *Atractus boettgeri* and *A. taeniatus* in southwestern Bolivia (Departments of Santa Cruz and Cochabamba) are morphologically similar and differ only in secondary sexually dimorphic characters (i.e., segmental counts) in males and females, respectively. Also, the color differences highlighted in McCoy's sample ($n = 3$) are associated herein with both conspicuous juvenile coloration and a tendency toward melanism in adult specimens (see also Passos et al. 2013a). McCoy (1971) provisionally recognized *A. emmeli* and *A. boettgeri* as distinct species on the basis of number of supralabials (seven in *A. emmeli* vs. six in *A. boettgeri*). However, he also stated: "Moreover, one of the specimens of 'taeniatus' has 7 supralabials on one side, suggesting that more specimens will show this character to be variable" (McCoy 1971:316). We found that the range of variation of all features previously used to diagnose members

of the *A. emmeli* species complex (i.e., *A. boettgeri, A. emmeli, A. taeniatus,* and *A. paravertebralis*) widely overlap each other and population frequencies are not fixed (Table 1; Figs. 2–7, 9–10). Especially in the case of the supralabials, there is a tendency for reduction to six scales among Bolivian populations, although a high level of polymorphism exists (Table 1).

With respect to continuous characters with high variance, we found variation in ventral scale numbers as the main axis of morphological variation, with individuals displaying larger values for nearly all groups sampled. The possible causal relationship between the number of segmental counts (a reflection of the number of vertebrae through somitogenesis process; see Alexander and Gans 1966; Lindell 1994) with environmental variables such as temperature and humidity (Fox 1948; Fox and Fox 1961) frequently has been used to explain meristic geographical variation in Neotropical snakes. This pattern is generally associated with localities at low latitudes, where temperature and humidity are higher than in more southerly regions (Hoge et al. 1976; Passos et al. 2005a,b, 2013d; Passos and Fernandes 2009). The distribution of this feature among the *Atractus emmeli* complex is apparently correlated with local temperature and humidity regimes on the basis of models performed (Fig. 12; Fig. S2 in the Supplemental Materials available online). Although it does not follow a linear cline gradient of variation, the populations from Mato Grosso, Brazil (on both north and south portions of Parecis Plateau), present higher averages of segmental scales than do other rainforest members of *A. emmeli* complex (Table 1).

The most divergent population in the *Atractus emmeli* complex, based on phenotypic characters (both discrete and continuous), was from Mato Grosso in Brazil (named herein as *A. stygius*). This is the only population of the *A. emmeli* complex not previously named. These individuals have larger body sizes, larger numbers of ventral and subcaudal scales, usually uniformly black dorsum (frequently obscuring the pale parietal band in adults), and hemipenes with narrow sulcus spermaticus (see comparisons). In fact, some of these characteristics more closely resemble *A. albuquerquei* (a species occurring sympatrically in some localities of the Brazilian Cerrado) than *A. emmeli*. However, *A. albuquerquei* is very conspicuous in having a uniformly cream belly, six supralabials, usually six infralabials, absence of parietal pale band, and presence of the hemipenial naked pocket (see Zaher et al. 2005 and also comparisons provided herein), and none of these features occur in *A. stygius*. Unfortunately, to the best of our knowledge, no tissue samples are available from *A. stygius* or from populations of *A. emmeli* from Bolivia and Peru, precluding inferences on their phylogenetic relationships at the moment. Without a robust phylogeny we cannot establish if *A. stygius* is more closely related to *A. emmeli* or to *A. albuquerquei,* although we anticipate that it is more likely that *A. stygius* is the sister species of *A. albuquerquei*. Although obtaining geographically representative samples for some species with secretive lifestyle is difficult, we suggest that the study of additional character systems can greatly aid in defining the taxonomic status of the aforementioned taxa (see Passos et al. 2017). Based on the results of the present study, we believe that niche modeling or niche overlapping analyses may represent feasible complementary approaches to corroborate species boundaries in the absence of accurate phylogenetic hypothesis.

Areas with high values of environmental suitability for *Atractus emmeli* do not overlap and are widely separated from the known records of *A. stygius* (Fig. 12). This suggests a considerable difference in the potential niches of the respective species, corroborating the phenotypic evidence of distinction of *A. stygius* from *A. emmeli* (Table 2; Fig. 12; Fig. S2 in the Supplemental Materials available online). Conversely, suitable areas for *A. albuquerquei* suggest a considerable potential sympatry of this species with *A. stygius* and a similar potential niche. Moreover, based on the records of *A. albuquerquei* provided by Zaher et al. (2005), there is at least one sympatric location for both species at Claudia municipality (see fig. 4, Locality 12 in Zaher et al. 2005:26). However, it is possible that some specimens previously identified as *A. albuquerquei* represent in fact *A. stygius*. Unfortunately, the first author could not find these specimens during the last visit to MZUSP collection and this suspicion must be corroborated in the future

Models for *Atractus albuquerquei* and *A. emmeli* indicate great differences in ecological niches of clades occurring in the Cerrado versus clades occurring in the Western Amazon–Andean foothills, suggesting a putative niche evolution in species of this group (Fig. 12; Fig. S2 in the Supplemental Materials available online). Although a low overlap in their projected environmental niches since the Last Glacial Maximum might suggest a mechanism for the diversification in this group (adaptation to the Cerrado savannas–gallery forests vs. humid–dry forests), the segregation of *A. stygius* from *A. emmeli* could be considerably older than the Pleistocene, as suggested by the diversification times of other clades of Squamata in the region (e.g., *Kentropyx;* Werneck et al. 2009). Alternatively, it may be related to the geomorphology formation of the Parecis Plateau, separated from other portions of the Brazilian Shield by tectonic shifts that largely predate the Quaternary (see Silva 1995; Werneck et al. 2009; Nogueira et al. 2011). Other endemic squamate species broadly sympatric with *A. stygius* at the Parecis Plateau include *Bachia didactyla* Freitas et al. 2011, *Ameiva parecis* Colli et al. 2009, and *Apostolepis striata* Lema 2004, and the discovery of this new *Atractus* species supports the idea that the Parecis Plateau represents one of the many natural biogeographical units within the vast and still poorly sampled central Brazilian savannas (see Azevedo et al. 2016). Nonetheless, such speculation still must be tested based against a robust time-calibrated phylogeny for the genus and, unfortunately, the fossil records of the group remain unknown.

Supplemental Material

Supplemental material associated with this article can be found online at https://doi.org/10.1655/HERPMONOGRAPHS-D-18-00007.S1; https://doi.org/10.1655/HERPMONOGRAPHS-D-18-00007.S2; https://doi.org/10.1655/HERPMONOGRAPHS-D-18-00007.S3.

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APPENDIX

Specimens Examined

Countries are given in underlined capitals, states in capitals, municipalities in italics, and localities in plain text. Specimens for which we prepared hemipenes are indicated with an asterisk.

***Atractus albuquerquei* (*n* = 55).**—BRAZIL: GOIÁS: *Aporé*: Aporé Hydroelectric Power Plant (MNRJ 14370–76), *Chapado do Céu* (IBSP 58934), *Minaçu*: Cana Brava Hydroelectric Power Plant (MZUSP 13024, 13368–69), Cana Brava Hydroelectric Power Plant: Cavalcante (MZUSP 13365–67), Mineiros (MNRJ 24393); MATO GROSSO: *Apiacás* (MZUSP 11157), *Claudia*: Iracema Farm (MZUSP 11242), *Porto Estrela*: Serra das Araras Ecological Station: Serra da Araras (MZUSP 14126–27), *Rio Correntes*: Ponte de Pedra Hydroelectric Power Plant (MZUSP 17735–38); MATO GROSSO DO SUL: Canaã Farm (MZUSP 4586), *Três Lagoas* (IBSP 76820, MZUSP 4586); PARÁ: *Canaã dos Carajás*: Base do Níquel do Vermelho (MPEG 22183), *Curionópolis* (MPEG 25359–60), *Marabá*: FLONA Tapirapé-Aquiri (MPEG 23926–27), *Orilândia do Norte* (MPEG 20792), *Parauapebas* (MNRJ 18041), *Vila Nova*: Tomé-Açu–Paragominas road, near Timboteua River (MPEG 12946, holotype); TOCANTINS: *Goiatins* (MNRJ 20629); RONDÔNIA: *Jaru* (MZUSP 8679), *Machadinho d'Oeste* (MZUSP 21665), *Monte Negro* (IBSP 73957), *Nova Brasília* (MZUSP 8733–34), *Nova Colina* (MZUSP 8504, 8509), *Porto Velho*: Samuel Hydroelectric Power Plant (CHUFC 1482–84), Vila Cachoeira do Samuel (MNRJ 3028), Jirau Hydroelectric Power Plant (MZUSP 18890, 19993, 20821, 20864, 21113, 22138), *Santa Barbara* (MZUSP 8678, 8777–78).

***Atractus emmeli* (*n* = 48).**—BOLIVIA: BENI: *Guayaramerin* (USNM 123971*–72), *Yacuma*: Beni Biological Station: Yacuma (CBF 434), Ballivián: *San Marcos*: Río Negro (MNKR 3718*–19); LA PAZ/COCHABAMBA: Yungas (BMNH 1946.I.6.29, holotype of *Atractus boettgeri*); LA PAZ: *Campolican* (BMNH 1895.II.21.26), *Charobamba* (BMNH 1895.II.21.22–25), *Sud Yungas*: Covendo Mission range (MSNG 28873, holotype of *Atractus balzani*), *Iturralde* (CBF 765a,b), Maldidi (CBF 758), *Moxos*: San Lorenzo (CBF 992); PANDO: Manuripi National Wildlife Reserve: Malecon camp (ACF 21); SANTA CRUZ: *Andrés Ibañez*: El Vallecito (CBF 008, 3717), 8.5 km from Santa Cruz de la Sierra–Cochabamba road (MNKR 321), Campus Universitario: *Santa Cruz de la Sierra* (MNKR 17); BRAZIL: ACRE: *Porto Walter* (MZUSP 7386); RONDÔNIA: *Porto Velho*: Samuel: Hydroelectric Power Plant (CEPB 1700–01), Jirau Hydroelectric Power Plant (MZUSP four specimens not catalogued*). PERU: Unknown locality (MUSM 2313); CUSCO: *Convención*: Camisea (MUSM 3467); LORETO: *Coronel Portillo*: Pucallpa (MUSM 2653, 3101); HUÁNUCO: Tingo Maria, Universidad Agraria de la Selva, vicinity of the Huallaga River (USNM 193730–35, 193736*, 193737–39); JUNÍN: *Tarma*: Yurinaqui Alto (MUSM 2644, 11144); LORETO: *Tromperos* (MUSM 27402).

***Atractus stygius* (*n* = 10).**—BRAZIL: MATO GROSSO: *Brasnorte*: Craveri River small hydroelectric central of Bocaiúva (UFMT 8137–38, 8139*, 8140–42, paratypes, MNRJ 26734*, holotype), *Claudia*: Continental Farm (UFMT 3949, paratype), *Jaurú*: Vale de São Domingos (MNRJ 26735, paratype), São Nicolau Farm: Juruena River (UFMT 9116, paratype), *Sapezal*: Juruena River: small hydroelectric center at Segredo (MZUSP 20667, paratype).